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MELBOURNE

STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

VII. THE LONGOARCUATE SKULL

By R. TUCKER*

(*Manuscript received June* 22, 1955)

Summary

An analysis is made of the morphofunctional relations of the longoarcuate skull, using the skulls of lagomorphs and rodents.

Then the paper considers the morphology of the premaxillary node as well as the absence of the supraorbital node, the anterior translocation of the squamosal node, and the development of the preorbital node. Then details of the fronto-premaxillary junction and complicated morphofunctional connections in the preorbital node are given.

Finally, the vectorial analysis of the structure of the longoarcuate skull is discussed.

I. INTRODUCTION

The study of the longoarcuate skull presented here is based on the methods described in Part I of this series (Tucker 1954*a*), and is meant as the demonstration of factual material which will serve to build up comparative conclusions in Part IX of this series (Tucker 1955*c*). The morphofunctional characteristic of the longoarcuate skull is accentuated by various features of premaxillary, squamosal, and preorbital nodes which are subsequently dealt with. The terms "transposition" and "transformation" refer to the morphofunctional pattern which has emerged from the previous studies.

II. THE PREMAXILLARY NODE IN THE LONGOARCUATE SKULL

In the longoarcuate skull almost every bone displays adaptive changes towards the transmission of stresses to distant points. Among these, the development of the premaxilla is most characteristic (Tucker 1954*b*). The longoarcuate skull, in general, has a marked tendency to shift the transmission of stresses in the supraorbito-maxillary tract from the maxilla, which is the sole transmitter of stresses in the breviarcuate skull, towards the premaxilla. The latter, by virtue of its elongated and strong frontal process, forms the essential part of the supraorbito-maxillary tract (Plate 1, Figs. 1, 2, and 3). The consequence of that is a decrease of this type of stress in the longoarcuate maxilla, which may be observed in Leporidae by the formation of irregular trabeculae which are unable to

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transmit stresses of importance in any one direction (Plate 1, Fig. 6). Another factor influencing the morphology of the maxilla in small rodents is the anterior translocation of masticatory musculature. The latter may cover the lateral surface of the bone, causing, as in the guinea pig, the formation in the upper part of the maxilla of a semicircular maxillary margin (Plate 1, Fig. 7*b*) which articulates with the frontal process of the premaxilla (Plate 1, Fig. 7*a*).

In the longoarcuate skull, the premaxillo-maxillary tract is toothless. Accordingly, in the facial region, there are no laterally directed stresses. The lack of these forces, which usually act between the upper and mandibular rows of teeth, has influenced the different construction of the hard palate, which in longoarcuate conditions is often short and narrow (Plate 1, Figs. 8 and 9).

The nasal bones do not join the maxilla. They are situated high, and their main function is to cover the nasal cavity. Usually there are three contacts of the nasal bone, namely, with the premaxilla, maxilla, and frontal bone; however, in guinea pigs and Leporidae there is only one—with the frontal bone. In the longoarcuate skull the maxillo-nasal connections are, as a rule, lost, and the premaxillo-nasal connection, if present, often does not reach the stage of sutural junction. In other words, the stresses in the premaxillae in this type of skull influence the form of the premaxillo-maxillary suture. On the level of the vomer in the premaxillo-maxillary suture are developed the sutural lamellae (Plate 1, Figs. 8 and 9). Their number varies, and the lamellae are large in *Lepus* but small in guinea pigs. The palatine process of the premaxillary bone is usually very long (Plate 2, Fig. 11*a*), and is also developed in a way different from that in the breviarcuate skull.

The body of the premaxilla is compact and high, and much shorter than its processes. The frontal process is very long (Plate 1, Figs. 1-5). In most of the planoarcuate skulls it is shortest (e.g. ruminants), medium in breviarcuate types (e.g. Canidae), and longest in longoarcuate types (e.g. Lagomorphae). The frontal process in ruminants reaches only to the nasal bone. In breviarcuate skulls the process is longer and tends to penetrate between the nasal bone and the maxilla, but never reaches the frontal bone. In longoarcuate types the frontal process of the premaxilla articulates with the frontal bone. This contact, as well as the relations of the frontal process to the nasal and maxillary bones, is very characteristic of the lagomorphs. (In primates, whose characteristic is the marked transposition of the neuro- and splanchnocranium with regard to each other, the substitution of the dorso-caudal, or even dorsal position, of the neurocranium for the caudal position in other mammals is accompanied by great variety in the extension of the premaxillary bone which may reach only to the nasal bone, or it may partly separate the nasal bone and maxilla, or it may reach the frontal bone.)

III. THE MAXILLARY AND SUPRAORBITAL NODES

Important transformations in the longoarcuate type occur in the maxillary and supraorbital nodes. The lack of laterally directed stresses at the level of the alveolar process is well reflected in the reduction of the palatine process of the maxillae, as well as in the absence of molar recesses, and by the formation of very large premaxillary incisurae (Plate 1, Fig. 9). (The molar recesses are clearly visible in Canidae and certain other carnivores: this is an effect of the laterally directed stresses in the maxillary node; these change the position of the teeth, forming deep recesses.)

Lack of molar recesses is seen in Leporidae, while *Cavia cobaya* presents a slight variant. In *Cavia*, the hard palate, which is short, and the maxillary alveolar processes are developed similarly to those in the Leporidae. However, while the upper and mandibular rows of teeth cover one another exactly, their longitudinal axes slope from ventro-lateral to dorso-medial, thus producing changes in the maxilla and mandible. These changes are of local and secondary importance.

In *Cavia* (Plate 1, Fig. 8), the maxillary processes of the premaxilla and the incisor incisura are smaller than in Leporidae (Plate 1, Fig. 9). The frontal process of the premaxilla is a thin plate directed anteriorly and dorsally and connected caudally with the premaxillary process of the frontal bone. The frontal process of the premaxilla forms the lateral wall of the nasal cavity and supports the nasal bones.

The longoarcuate type of skull is characterized by the direct connection between the premaxillary and frontal bones and by the development of the fronto-premaxillary suture.

In *Lepus* (hares) and *Oryctolagus* (rabbits), the frontal process of the premaxilla not only joins the frontal bone, but penetrates it and finally rests between the processes of the frontal bone. These processes of the frontal bone number two, viz.:

(1) Lateral premaxillary process of the frontal bone (Plate 2, Fig. 12*a*), which is thin, long, and situated more laterally; and

(2) Inner premaxillary process of the frontal bone, which is shorter, compact, and located more medially (Plate 2, Fig. 12*b*). This process forms the supporting structure for the nasal bone together with the frontal process of the premaxillary bone.

The whole picture of the supraorbital node is completed by the presence of the frontal incisure (Plate 2, Fig. 12*c*) which is limited laterally and internally by the abovementioned processes. In the incisure is located the sutural part of the frontal process of the premaxillary bone. The sutural part is broader than the basal part of the frontal process of the premaxillary bone, which together with the maxillary process of the nasal bone and the frontal bone form the well-developed gomphic suture (gomphus).

The stresses which are located in the premaxillary node are transmitted towards the frontal bone. The penetration of the frontal process of the premaxillary bone into the frontal bone provides clear evidence of this. Among the sutures which exist, the marked compressions are in the gomphic and the gradic suture.

IV. The Zygomatic Arch

In the rabbit and guinea pig there is no direct contact between the frontal bone and the zygomatic arch. The frontal process of the malar bone and the postorbital process of the frontal bone are generally not developed. In some skulls (e.g. Leporidae) the postorbital process may remain a small structure and never contact the zygomatic arch (Plate 2, Fig. 13*b*). In this case the postorbital process is not shaped by the stresses from the postorbital tract but is translocated under the influence of the large optic bulb and forms the superior limitation of the eye bulbs (cf. Leporidae). (The position and the name of the postorbital process in Leporidae may be misleading. I am using the name "postorbital process" as it is used in previous and subsequent papers, and since this process is usually described in connection with commonly studied skulls, for instance in Canidae, I think that for comparative purposes it is better to keep the same name even if a slight variation from the accepted pattern occurs. However, another description is also possible, namely to change the name to "supraorbital" indicating that it corresponds to the postorbital processes in other skulls.) The supraorbital node does not participate in the work of the squamosal node and zygomatic arch, as in the breviarcuate type. Only in the longoarcuate group is the zygomatic arch bent inferiorly. The inferior margin of the zygomatic arch may be situated on the level of the mandibular dentition as in *Cavia cobaya.*

In the longoarcuate skull the zygomatic arch is not supported by the frontal bone, and the supraorbital node changes its shape under the action of the masseter. Simultaneously, the malar bone becomes very large and builds up its connecting surface with the lacrimal bone.

The stresses which are located in the premaxillary node are transmitted towards the frontal bone. The penetration of the frontal process of the premaxilla into the frontal bone was described above.

As previously mentioned, the supraorbital node does not participate in the work of the squamosal node and zygomatic arch as in the breviarcuate type. The size of the malar bone and the changes in connections between the maxillary and the malar bone introduce a new element into the conditions of this part of the skull. The necessary contact with the frontal bone is made through the lacrimal bone in the guinea pig and partially in this way in the rabbit. Accordingly, the zygomatic arch and the frontal bone create another node situated more anteriorly (relative to the supraorbital node). It is the preorbital node (nodus preorbitalis—Plate 2, Fig. 13; Plate 3, Figs. 14 and 15).

V. THE PREORBITAL NODE

The preorbital node is characteristic of the longoarcuate skull. This node has many more bony elements than the supraorbital node. The frontal, lacrimal, maxillary, and even the premaxillary bone takes part in its formation. However, while there is one frontal process from the lacrimal bone in Leporidae, there are two in the guinea pig. The largest is the fronto-maxillary process, (Plate 3, Fig. 15*d*), the smaller is the frontal process (Plate 3, Fig. 15*e*). The fronto-maxillary process of the lacrimal bone overlaps the nodular process (Plate 2, Fig. 12*d*; Plate 3, Figs. 14 and 15*b*), anteriorly and laterally, the frontal process overlapping from the lateral and posterior sides. In addition, the whole frontal margin of the lacrimal bone is closely connected with the frontal bone. From the premaxillary bone originate its long and narrow (in Leporidae) or more massive (in *Cavia cobaya*) frontal process of the premaxilla (Plate 1, Fig. 7*a*). In Leporidae a few trabeculae of the trabelcular-maxillary net join the lacrimal bone.

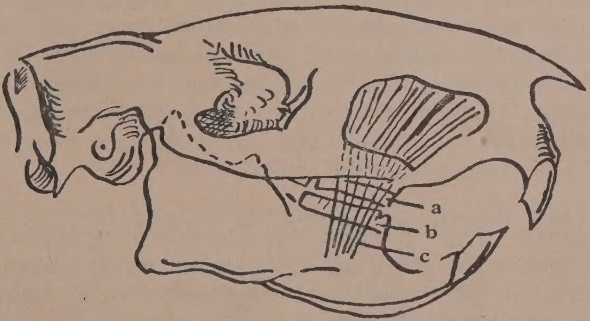

Fig. 1.—Diagram of the skull of a rodent showing the relations of the alveolar processes to the masticatory muscle. *a*, Maxillary alveolar process; *b*, mandibular alveolar process; *c*, muscle.

Simultaneously with the development of the preorbital node the insertions of the masseter are translocated anteriorly, or new muscular units, such as maxillo-mandibular muscle, develop. In consequence of this last movement, the alveolar process of the maxilla is not situated anteriorly to the masticatory muscles, but is in the centre of muscular action (Fig. 1). This relative transposition now affects the action of the mandible. The translocation of muscular insertions exempts the zygomatic arch from much of the stress.

The transpositions of preorbital and zygomatic regions cause structural changes in other parts of the cranial structure. Accordingly, the elongation (caused by the anterior movement of the squamosal node) of all structures which are situated caudally from the squamosal node and zygomatic arch is very characteristic for the longoarcuate skull.

VI. The Squamosal Node

In the Carnivora, the postprocessial sustentaculum is rather short and the temporal crest is situated near the zygomatic process of the squamosal bone. The squamosal node of the longoarcuate skull is translocated not less than the supraorbital node. The translocation is in the same direction —towards the orbits. These translocations result in diminution of stresses in the dorso-caudal part of the skull, which, in combination with the small size of these animals, causes the morphological picture described below.

In *Cavia cobaya* the squama of the squamosal bone is shaped as a long curved process whose connections with other bones are very loose (Plate 3, Fig. 16). The tegmental part of the skull is smooth; the cristae are very small or disappear. The bony transformations of the sutures in this region of the longoarcuate skull occur relatively late. On the contrary, the catalysing effect of stresses on the development of the sutures is clearly visible in other types of skull. In the occipital region of the longoarcuate type, the development of the sutural lamellae is very poor. The elongated squama of the squamosal bone on its long jointing surface with the parietal bone has no lamellae at all. The developed sutural structures are present only in the terminal part of the squama. This part is enlarged and situated low in the region of the petrosal bone behind the external auditory meatus. All these changes are the result of the anterior transformation of the squamosal node and the subsequent diminution of the stresses in the posterior part of the skull.

VII. The Basal Part of the Facial Region

The changes in the basal part of the longoarcuate facial region are also numerous. The problem of junction between the squamosal and maxillary nodes is essentially the same as in breviarcuate skulls, but the different translocations caused new structural conditions. The distance between the two nodes is rather small and all molars are about equally stressed. The axis of dentition may be changed as in *Cavia cobaya* (Plate 2, Fig. 13). The topography and development of dentition show many planoarcuate features. The characteristic feature of the longoarcuate and planoarcuate skulls is the development of the adental margin. The adental margin is closely connected with the animal's way of life which involves a non-carnal diet of non-motile organisms, of which the plant is commonest. Incisors can be used to bite plants and to cut trees, but their use for wrenching is impossible. Carnivora, on the other hand, can sink their teeth into living tissues and tear pieces from large bodies.

The correlation between the structure of the alveolar process and the cranial transformation is obvious. The lowest part of the alveolar process in Carnivora is at the level of P^4; the highest part is the P^{1-2}. In this part the longoarcuate and often the planoarcuate skulls lose the teeth. Instead of teeth, the adental margin develops, making a junction between the well-developed premaxillary and maxillary nodes. In the breviarcuate skull, the stresses accumulate in the caudal part of the alveolar process. The tendency to lowering of the caudal part of the alveolar process is indicated in many planoarcuate skulls of insectivores. Wherever there is division of function in the alveolar process, changes occur in other regions of the skull as well. The adental margin forms the highest degree of similarly directed changes. In the longoarcuate skull, the maxillary node is not as distinctly circumscribed as in the breviarcuate skull. In the guinea pig, the posterior trabecula becomes a small, thin lamella without any mechanical importance. The superior row of dentition, the anterior trabecula, and the squamosal node are situated in nearly the same line. In consequence, the perpendicular lamina of the palatine bone is not as elongated as in Carnivora, and its connections with the sphenoid and presphenoid bones are much weaker.

The above outline of the morphology of the basal part of the facial region shows some striking similarities between the planoarcuate and longoarcuate skull, especially as regards the distribution of stresses which may arise in the maxillary node. It can be of special importance in the eventual detailed consideration of the ways in which the hypothetic dispersed stresses of the primitive planoarcuate skulls (see Part VIII of this series (Tucker 1955*a*)) become circumscribed or increased in particular areas of the whole structure.

VIII. THE BASIS OF THE SKULL

In the longoarcuate skull the perpendicular lamina is not shaped by horizontal tensions; it is wholly dependent upon the influence of the pterygoid muscle. The anterior trabecula is well developed and creates the main tension route between the alveolar process and the squamosal node. The second trabecula is situated medially to the first.

In the hare, the axis of the alveolar process is saggital, as in the breviarcuate type. The maxillary node demonstrates the tendency to limit the region of stresses. It is emphasized by the direction of the dental roots and the axes of the alveoli. The roots of the middle teeth are perpendicular but the terminal teeth have roots directed medially. The zygomatic arch is very short and the maxillary node is situated beneath the preorbital node. The perpendicular lamina of the palatine bone is large, with extensive connections to the sphenoid. The palato-sphenoidal connections are transformed under the influences which result in the dorsal translocation of the squamosal node.

The transformation in the spheno-occipital junction differs in the breviarcuate skull, where the squamosal node is translocated caudally, from those cases in which the squamosal node is situated anteriorly, as in the longoarcuate skull. In the longoarcuate skull, the spheno-occipital suture is weak while in Leporidae all sutures surrounding the occipital bone are poorly developed. Exposed trabeculae are developed in the hindmost part of the skull (Plate 3, Fig. 17) as in the maxilla of Leporidae.

The squama of the squamosal bone is connected with the parietal bone more closely than in the guinea pig. The sutures and junctions of the occipital bone with the parietal, squamosal, and sphenoidal bones show no special adaptations.

This region of the longoarcuate skull, in addition, is characterized by the following morphological features. The zygomatic process of the squamosal bone in the rabbit is bent inferiorly and has a deep groove (Plate 3, Figs. 18*b*, 19*b*) for articulation with the temporal end of the malar bone. The squama of the squamosal bone is rather short and forms, on its caudal end, a very long process known as the occipital process of the squamosal bone. In the rabbit the malar bone and zygomatic process of the maxilla meet. In the guinea pig, the malar bone is short, its caudal end developing the semi-sinus. Anteriorly the malar bone joins the zygomatic process of the maxilla, which is divided in its anterior part (Plate 3, Fig. 15*f*).

The abovementioned structural features are described in order to show that the shifting of the squamosal node caudally in the breviarcuate skull (see Parts III-VI of this series (Tucker 1954*c-f*)) and the translocation of the same node anteriorly, as in the longoarcuate skull, results in morphological differences in the neurocranium which are closely related to them. Furthermore, different positions of the squamosal node reflect upon the zygomatic arch. The relation between the zygomatic arch and the maxillary node in different types of skull is analysed in Part IX of this series (Tucker 1955*b*).

IX. DISCUSSION

The question of the deep transformations of main nodes in the longoarcuate skull still requires more investigation and elucidation. The role of the adental margin seems to be important in the transformation of the cranial structure. Pocock (1951, p. 2) described in Felidae, as one of the most characteristic cranial features, the presence of "considerable post-canine space between the jaws which is accentuated by the up-curvature of the anterior part of the mandible carrying the incisors and canines. The function of this is to give deep penetration to the canine teeth in killing prey. The space varies in dimensions in different species and is most manifest in the Clouded Leopard (*Neofelis*). In the Hunting Leopard (*Acinonyx*) which does not seize its prey with its mouth, the space, on the contrary, does not exist when the jaws are closed." The adental margin of longoarcuate skulls belongs, however, to a quite different phenomenon. It is really the extreme development of diastematic space which is always connected with the reduction of dentition or with translocation of dentition. Kubik (1952) described the very fast growth of the skull of rodents in the sagittal direction. These observations may have a relation to the formation of the nodes and tracts of the longoarcuate skull; however, the ontogenetical aspect of the differentiation of the functionally crucial points in this type of cranium belong still to future problems.

One of the main factors influencing the translocations and transformations of nodes in the longoarcuate skull may be the migration of the masseter in rodents. In the more primitive condition, the masseter is developed similarly to those of other mammals, and is divided into a more lateral portion and the medial part. In more advanced rodents both of these parts of the muscle obtain extra insertions. The lateral part may extend towards the face, and the medial part passes out of the orbit through the much enlarged infraorbital canal (Young 1950, p. 621-2). The anterior translocations of the masseter together with the poorly developed temporal muscle and the presence of the supraorbital node are closely related one to another. Moreover, the changes in the forces of muscles and new insertions of masseter really shorten the long principal arch of the skull, giving the type of conditions observed also in the ruminants.

X. Acknowledgments

I am greatly indebted to Professor P. D. F. Murray, University of Sydney, for much help in the preparation of Parts VII-IX of this series, as well as for his constructive criticism and encouragement. I also wish to thank Professor J. Francis, University of Brisbane, for his interest.

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Explanation of Plates 1-3

In all figures the single arrow points towards the anterior part and the double arrow towards the dorsal part of the structure.

Plate 1

Fig. 1.—The longoarcuate skull. The premaxillary bone of the guinea pig. *a*, Frontal process.

Fig. 2.—The longoarcuate skull. The premaxillary bone of the mouse. *a*, Frontal process.

Fig. 3.—The longoarcuate skull. The premaxillary bone of the rabbit. *a*, Frontal process.

Fig. 4.—The breviarcuate skull. The premaxillary bone of the cat. (Contrast figure with Plate 1, Figs. 1, 2, and 3.) *a*, Frontal process.

Fig. 5.—The planoarcuate features. The premaxillary bone of *Isoodon obesulus*. *a*, Frontal process.

Fig. 6.—The trabecular structure of the maxilla and the position of the nasal bones in the rabbit.

Fig. 7.—The premaxillo-maxillary relations in the guinea pig. *a*, Frontal process of the premaxillary bone; *b*, maxillary semicircular margin; *c*, maxilla; *d*, premaxilla; *e*, nasal bone.

Fig. 8.—The structure of the palate in the longoarcuate skull of the guinea pig.

Fig. 9.—The structure of the palate in the longoarcuate skull of the rabbit.

PLATE 2

Fig. 10.—*a*, Recessus molaris in the dog.

Fig. 11.—Guinea pig. *a*, Palatine process of the premaxillary bone.

Fig. 12.—Rabbit. *a*, Lateral premaxillary process of the frontal bone; *b*, inner premaxillary process; *c*, incisura; *d*, nodular process of the frontal bone.

Fig. 13.—Rabbit. *A*, alveolar process; *B*, frontal bone. — *a*, Preorbital node; *b*, postorbital process.

PLATE 3

Fig. 14.—Preorbital node of the rabbit. *a*, Nodular process of the frontal bone; *b*, external premaxillary process of the frontal bone; *c*, lacrimal process of the frontal bone; *d*, lacrimal bone; *e*, maxilla.

Fig. 15.—Preorbital node of the guinea pig. *a*, Frontal process of the premaxillary bone; *b*, nodular process of the frontal bone; *c*, maxilla; *d*, fronto-maxillary process of the lacrimal bone; *e*, frontal process of the lacrimal bone; *f*, zygomatic process of the maxilla.

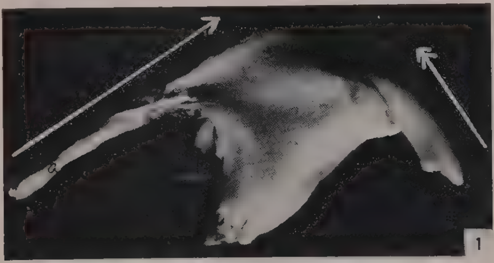
Fig. 16.—Squama of squamosal bone of guinea pig (left side).

Fig. 17.—Occipital part of the skull of the rabbit.

Fig. 18.—Squamosal bone of the rabbit. *a*, Zygomatic process; *b*, groove of the zygomatic process; *c*, occipital process (basal part only); *d*, squama of the squamosal bone.

Fig. 19.—Squamosal bone of the rabbit. *a*, Zygomatic process; *b*, groove of the zygomatic process; *c*, occipital process; *d*, squama of the squamosal bone.

FUNCTIONAL AND ANALYTICAL CRANIOLOGY. VII



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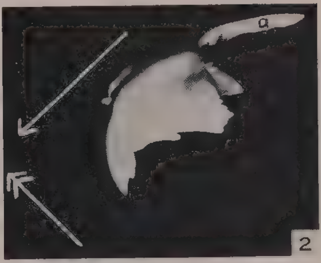

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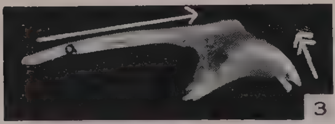

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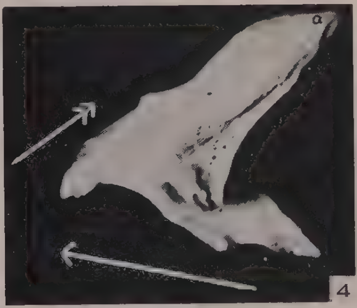

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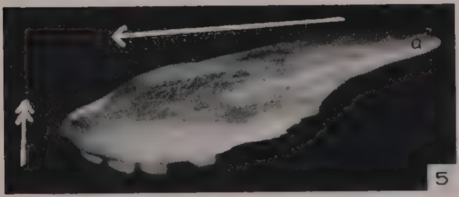

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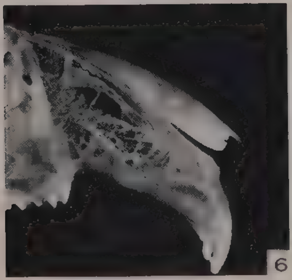

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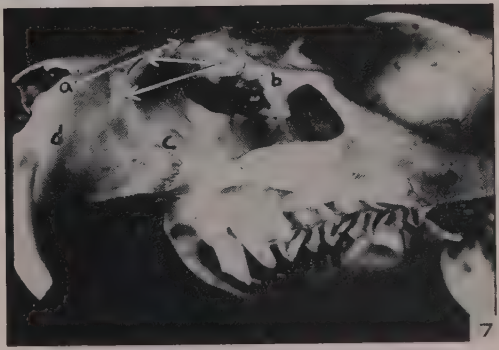

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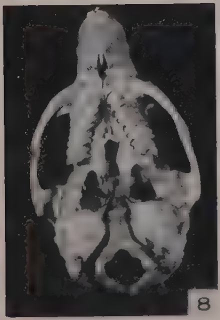

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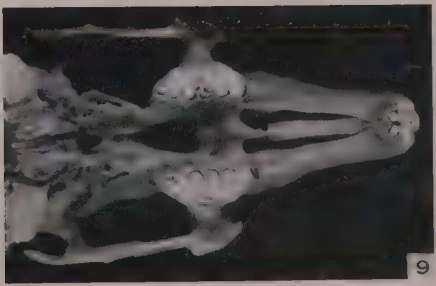

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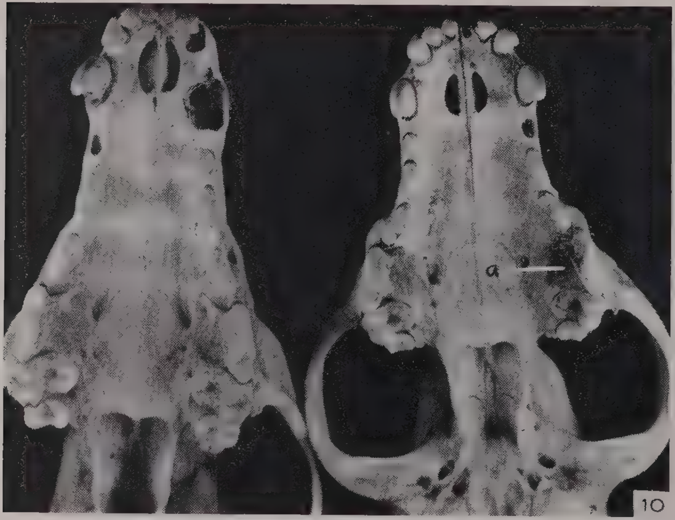
FUNCTIONAL AND ANALYTICAL CRANIOLOGY. VII



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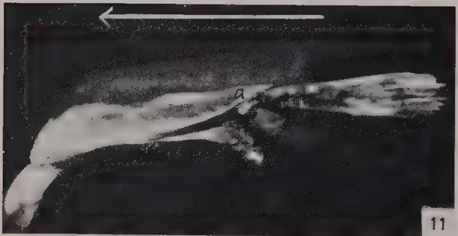

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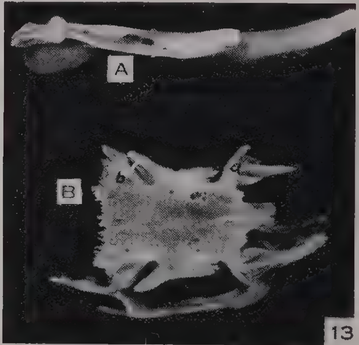

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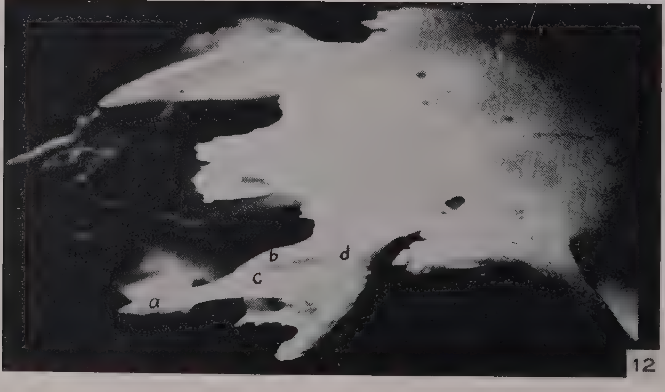

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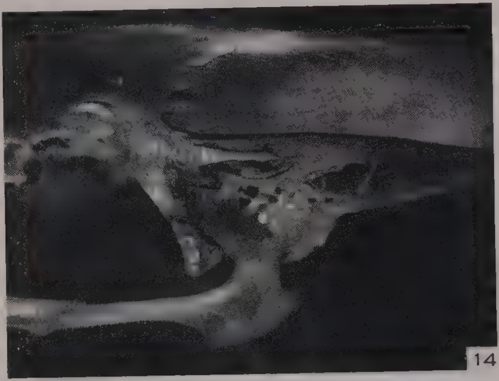
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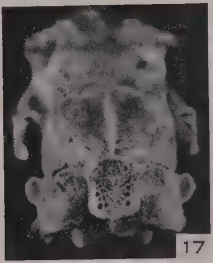
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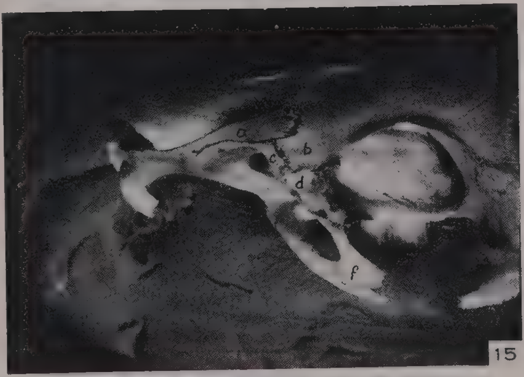

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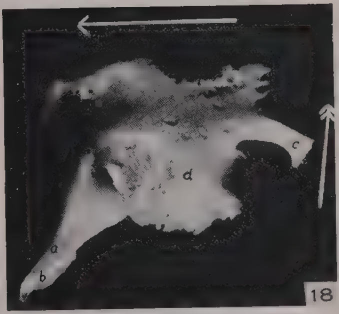

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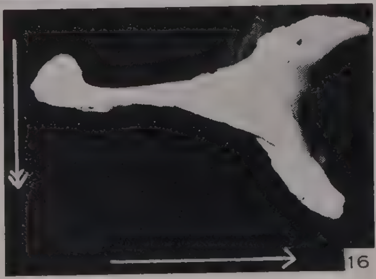
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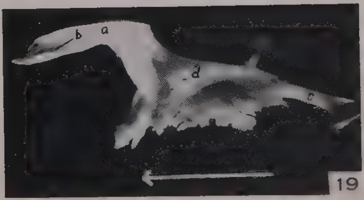

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STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

VIII. THE PLANOARCUATE SKULL

By R. TUCKER*

(*Manuscript received June* 22, 1955)

Summary

The planoarcuate skull is analysed in comparison with previously described types of crania. The extraordinary plasticity of the planoarcuate skull is pointed out, and explained in analytical and functional terms. The systematic and morphotical position of the mesozoic skull is discussed. The primitive planoarcuate skull, as well as advanced planoarcuate adaptations, are described. Certain similarities between the mammalian planoarcuate skull and the mechanical features of some reptilian skulls are pointed out.

I. GENERAL CHARACTERISTICS

The most remarkable transformations in the planoarcuate as compared with the breviarcuate and longoarcuate skull are changes in the orbit, supraorbital node, and in the zygomatic arch. The morphology of the alveolar processes is closely connected with the dispersion of stresses. The stresses in the planoarcuate skull are great but local, and do not provoke the formation of accessory structures; however, they influence the increase of existing bony masses. Hence the planoarcuate skull often demonstrates a relatively large quantity of bony tissue. The massive maxillary structure develops in Equidae into the maxillary (facial) crest, and in ruminants into the maxillary (facial) tuberosity (Figs. 1*a* or 2*a*).

The shape of the planoarcuate skull may vary widely, but always shows the massive bony tissue accumulated in the alveolar processes.

The development of the brain in primates and the differentiations of the tegmental part of the cranium in many planoarcuate skulls emphasizes the relative freedom of the cranial roof from the morphogenetic stresses which originate from the masticatory muscle; and also that the character of the relations between the maxilla and mandible is more constant than other functional relations in the planoarcuate skulls. The transmissive structures in the splanchnocranium are not developed, and the path of the stresses between the splanchno- and neurocranium is weakly developed. In the planoarcuate type, the neurocranium is situated either as an elongation of the splanchnocranium (most of Ungulata) or is moulded into a convex brain container as in primates. The regions in the planoarcuate skull which are not influenced by the circumscribed stresses may evolve in such independent directions that they do not appear as part of the same picture (e.g. the human brain case). This is made possible by the development of much bone in the parts of the skull more directly affected by the

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muscles of mastication. The planoarcuate skull exhibits one extreme (bony tissue in abundance) while some of the breviarcuate skulls display the opposite extreme (bony tissue very scarce). The relations (if any) between the amount of bony substance in the splanchnocrania of various functional types of skulls and the different kinds of jaw movements have not, to my knowledge, yet been investigated.

II. The Nasal and Maxillary Bones

The character of the planoarcuate skull is clearly demonstrated by the structure of the nasal, maxillary, premaxillary, lacrimal, and malar bones. The nasal bones in many planoarcuate skulls show a tendency to closer connections between them and the median septum of the nasal cavity. Thus, in sheep, the nasal bones are connected with the vomer by means of the strong median septum. In the breviarcuate skull, the nasal bones are situated horizontally and form the bar opposing the eccentric action of the mandibular teeth. In longoarcuate skulls, the nasal bones have lost their connections with the maxillary bones. In planoarcuate types, the nasal bones are more or less convex and contact the maxilla. In planoarcuate skulls, the dental condition creates a vector directed dorsally. This force influences the roof of the nasal cavity. As a result of the presence of two differently directed components of stress (horizontal and saggital), the nasal bone demonstrates in planoarcuate types two clearly divided faces:

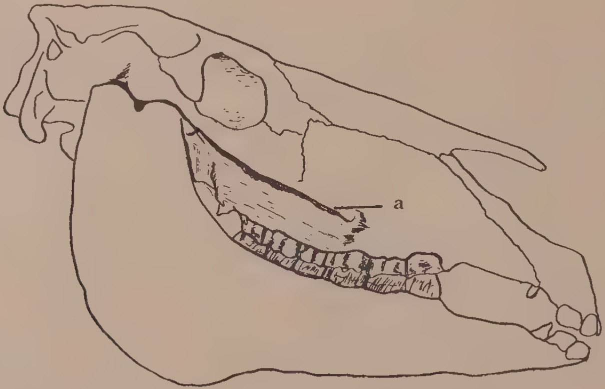


Fig. 1.—Skull of a horse. *a*, Maxillary crest.

(1) The maxillary face of the nasal bone. This face is situated in the same plane as the lateral face of the maxilla and forms its natural prolongation, and

(2) The tegmental face of the nasal bone. This is situated in the horizontal plane.

The two faces are separated by the interfacial line. The angle between the faces creates the best conditions for the dissipation of those stresses which pass in a direction from a ventro-external to dorso-medial. The tendency to the dorsal translocation of the roof of the nasal cavity caused by the above vectors is opposed by the well-developed median septum and its connections with the nasal bones.

In planoarcuate skulls the splanchnocranium contacts the neurocranium in a different way from that of the breviarcuate skull. While, in Carnivora, the maxilla is rather elongated caudally into the orbit, the planoarcuate skull shows the lacrimal and malar bones situated anteriorly to the orbit (Plate 1, Fig. 1*e* and *f*). In connection with this translocation stands the division of the supraorbito-maxillary tract into the maxillary (Plate 1, Fig. 1*B*, *g*) and zygo-lacrimal parts (Plate 1, Fig. 1*B*, *e*; Fig. 3). These parts differ in origin, shape, and particularly, in function.

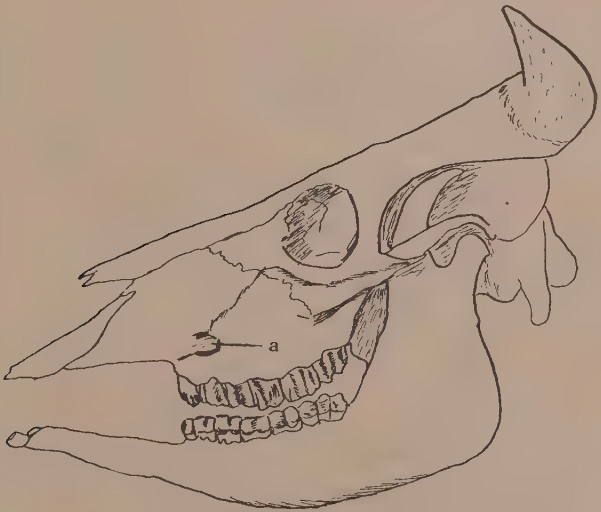


Fig. 2.—Skull of a cow. *a*, Maxillary tuberosity.

III. The Lacrimal and Premaxillary Bones

The development of the lacrimal bone and anterior translocation of the malar bone—especially of its superior ramus—in ruminants is connected with the laterally facing optic bulb. This is demonstrated in Plate 1, Fig. 1*B*, if it is compared with the anteriorly facing optic bulb in carnivores (Plate 1, Fig. 1*A*). In ruminants the optic bulb is also situated anteriorly. This type of supraorbito-maxillary tract in comparison with breviarcuate and longoarcuate skulls is characterized by the close connection between the supraorbital node and the malar bone. In the place of the postorbital tract in the breviarcuate skull is developed the postorbital (zygomatic) process of the frontal bone which joins the frontal process of the malar bone (Plate 1, Fig. 1*B*, *a*). The orbit is closed and the fronto-malar connections are rigid (in breviarcuate skulls elastic, and in longoarcuate non-elastic). As a result of this, the zygomatic process of the squamosal bone in many planoarcuate skulls is poorly developed. The maxillary insertions of the masseter are limited to the orbital region only. The squamosal squama is short (Plate 1, Fig. 1*B*, *b*).

The planoarcuate type of skull often demonstrates the convex, elongated premaxillary bone. According to the low stresses, the body of the premaxillary bone may be undeveloped (Plate 1, Fig. 1*B*, *e*). The lack of stresses in the premaxillo-supraorbital tract is emphasized by the naso-fronto-lacrimo-maxillary fissure (Plate 1, Fig. 1*B*, *d*).

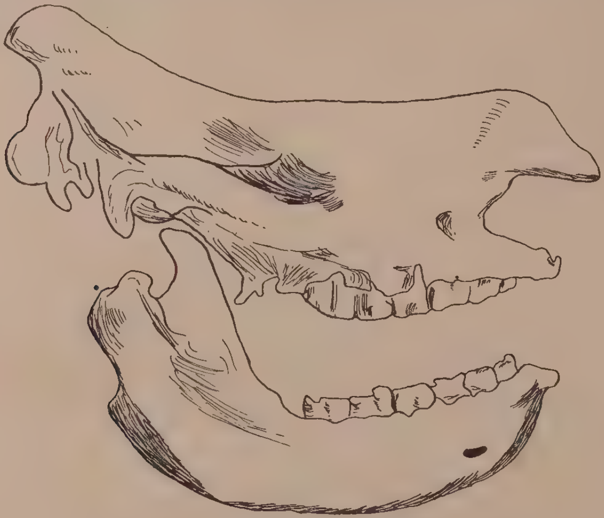


Fig. 3.—Lateral view of the skull of *Rhinoceros simus* (after Blainville).

IV. The Primitive and Advanced Planoarcuate Skull

Not all skulls which demonstrate the planoarcuate features have closed orbits with strongly developed fronto-zygomatic connections. As pointed out previously (Tucker 1954), the primitive type of mammalian skull may show many planoarcuate features. The structure of the alveolar process, the local character of stresses, and the distribution of elements of the splanchnocranium about the saggital axis exemplify clearly the condition in this type of skull. But the stresses in these crania, (for instance *Mammalia mesozoica*) are relatively very small. The zygomatic arch has no additional connections and often is undeveloped. Such skulls, especially characteristic of primitive mammals, are in fact the primitive skulls which in many points are similar to planoarcuate types, but none of the adaptive possibilities is developed to its greatest extent. In present day species, this type is often seen in the skulls of insectivora (with a trend to breviarcuate evolution) and in small mammals feeding on a variable diet. The skulls of the mesozoic (primitive) type show the beginning of breviarcuate adaptation in the slightly bent zygomatic arch, in the enlargement of connective surfaces between the zygomatic and squamosal bones, and in the development of the zygomatic process of the maxilla. The slight breviarcuate tendency is shown in the early formation of the major curvature of the skull, in the bending of the inferior edge of the alveolar process, and in the character of the body and processes of the premaxillary bones. Further details are added in association with the localization of the muscular insertions of the masseter and temporal muscles.

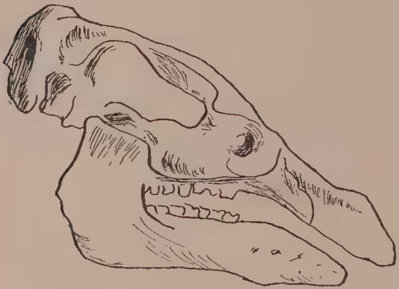
Parker (1885) in his study on the structure and development of the mammalian skull, has given some excellent descriptions and illustrations of the primitive planoarcuate development. In *Tatusia hybrida,* the zygomatic arch is nearly straight (Parker, Plate 6) ; in *Dasypus villosus,* concave (Parker, Plate 7) ; in a young *Cholopus hoffmani,* the malar bones tend to occupy an inferior position and have poorly developed connections with other bones; in *Cycloturus didactylus* the malar bone is absent altogether (Parker, Plate 10). The same conditions are described by Parker (1885) for pangolin (Parker, Plate 11) and for *Manis brevicauda* (Parker, Plate 12). *Orycteropus capensis* (Parker, Plate 14) and *Erinaceus europeus* (Parker, Plate 17) have the rudimentary zygomatic arch, while *Sorex vulgaris* (Parker, Plate 31), *Centetes caudatus* (Parker, Plates 32 and 33), *Hemicentetes madagascariensis,* and *Microgale longicauda* (Parker, Plate 35, Fig. 2) do not possess a zygomatic arch at all. The crania of all the abovementioned mammals belong to the primitive type of planoarcuate skull.

The planoarcuate skull often forms the object of palaeontological investigations. Accordingly, very good reproductions of this type of skull may be found in palaeontological papers and textbooks (cf. Gaudry 1862-1867; Abel 1921; von Zittel 1925-1932; Romer 1941, 1945).

The planoarcuate skull is so polymorphic in its functionally less important parts that it probably should be subdivided into a few exactly defined types. As examples of the various expressions of the planoarcuate conditions may be named the skulls of *Glyptodon, Scelidotherium, Megatherium, Plesiadapis* (Primates) ; *Manis, Tarsius, Notharctus, Homo sapiens fossilis* and *recens, Phenacodus, Toxodon* (Ungulata) ; *Elephas, Paleomastodon, Uintatherium,* and *Pyrotherium* (Pyrotheria) ; *Brontops* (Perrisodactyla) ; *Tapirus, Phacochoerus, Titanotherium, Manteoceras, Telmatherium, Coelodonta, Ovibus, Diceros pachygnatus, Criotherium argaloides, Sus erymantius* Ross and Wagner, *Mesopithecus pentelicus* Wagner, *Arsinotherium zitteli* (Baednell), *Megacerops robustus* Marsh, *Procervus variabilis* Alex, and others. The planoarcuate skulls of *Rhinocerus simus, Manatus australis,* and monkey are demonstrated in Figures 3 and 4 and also in Plate 1, Figures 2 and 3.

V. The Planoarcuate and Other Features in the Reptilian Skull

The discussion about the primitivity of any of the cranial differentiations in mammals must touch the problems of the composition of the skull of reptiles, especially in view of the fact that the mammal-like reptiles—



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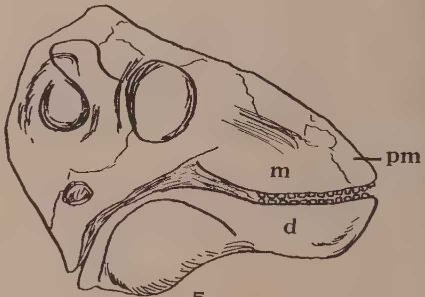

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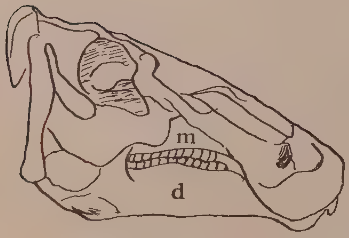

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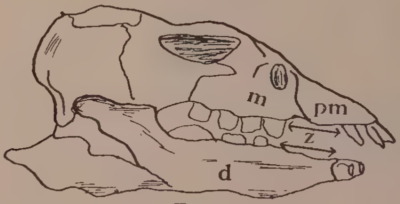

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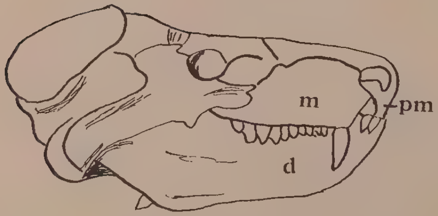

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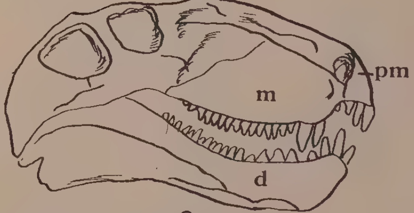

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Fig. 4.—Lateral view of the skull of *Manatus australis* (after Blainville).

Fig. 5.—The skull of *Delphinognatus* (after Romer). *m*, Maxilla; *pm*, premaxilla; *d*, dentale.

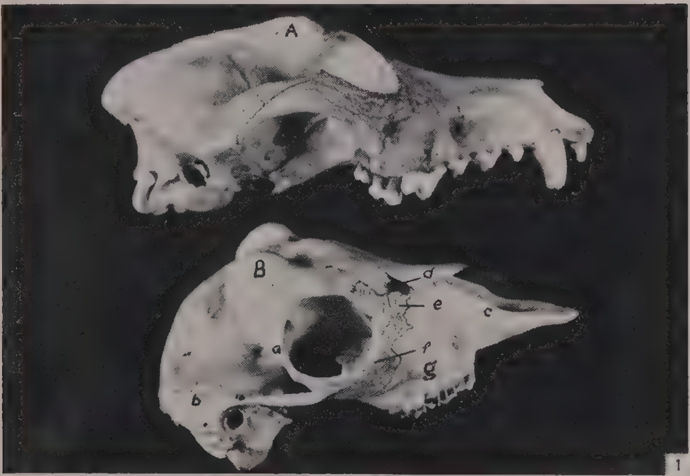
Fig. 6.—Skull of *Edmontosaurus* (after Romer). *m*, Maxilla; *d*, dentale.

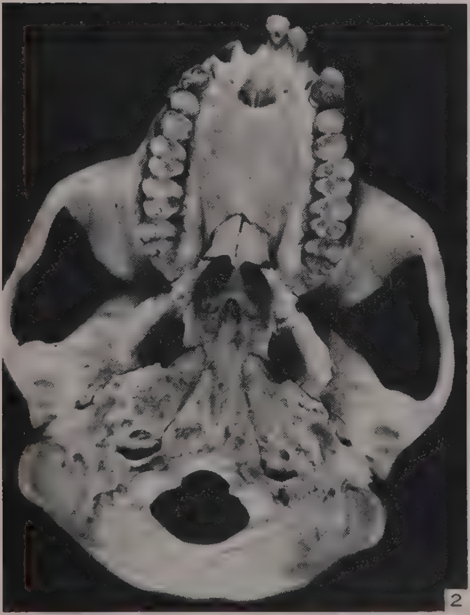
Fig. 7.—Skull of *Placodus* (after Romer). *m*, Maxilla; *pm*, premaxilla; *d*, dentale; *z*, adental margin.

Fig. 8.—Skull of *Cynognathus* (after Romer). *m*, Maxilla; *pm*, premaxilla; *d*, dentale.

Fig. 9.—Skull of *Dimetrodon* (after Romer). *m*, Maxilla; *pm*, premaxilla; *d*, dentale.

Synapsida—appear early in the history of this class (Romer 1945). Moreover, knowledge of the functional transformations in the reptilian skull can be of importance for the understanding of metamorphoses in the mam-





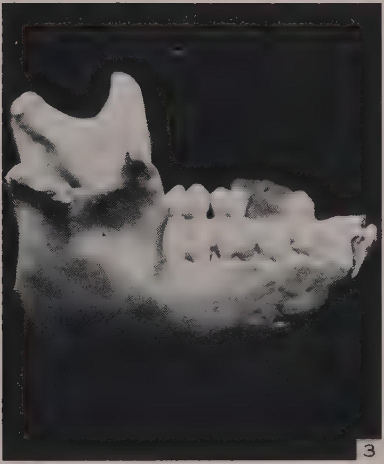


Fig. 1.—Position of the malar bone and the lacrimal bone in the breviarcuate and planoarcuate skulls. *A*, dog. *B*, goat. — *a*, Postorbital process of frontal bone; *b*, squamosal squama; *c*, premaxillary bone; *d*, naso-fronto-lacrimo-maxillary fissure; *e*, lacrimal bone; *f*, malar bone; *g*, maxilla.

Fig. 2.—Ventral view of the skull of a monkey.

Fig. 3.—Mandibular row of dentition in the monkey.

malian cranium. The initial structural stages may be very different from those in mammalia, as exemplified in the conditions caused by the topography and number of temporal openings. However, at present the functional and analytical craniology of reptiles is literally a *terra ignota*. For the latter reason, the reference to the reptilian skull is limited here to a few comparative remarks only. Even a superficial survey of the various types of reptilian skulls results in detection of the distinct planoarcuate features which, as in mammals, evolve in various directions. For instance, the skull of *Delphinognathus* (Tapinocephalia, Therapsida) (Fig. 5) has the dentale on the one hand and the premaxillary and maxillary on the other differentiated into two beams resting on one another. Moreover, the lack of diastemata, the anterior position of both beams, the dorsal position of the neurocranium, dorsal to the splanchnocranium, resemble the primate type of planoarcuate skull. The skulls of *Edmontosaurus* (Ornithopoda, Ornithischia) (Fig. 6) and *Placodus* (Placodontia, Sauropterygia) (Fig. 7) also exhibit various planoarcuate features. *Placodus*, to some extent, in the arrangement of planoarcuate features, resembles the functional relations in the ruminant variant of the mammalian planoarcuate skull (the beams of the dentale and the mandible are situated rather posteriorly with a well-developed adental margin), and, to some extent, the mechanical conditions in *Manatus* (Fig. 4) (diastemata), while the skull of *Edmontosaurus* has some similarity with the mammalian planoarcuate skull as seen in pigs.

In reptiles, which, like *Cynognathus* (Cynodontia, Therapsida) (Fig. 8) or *Dimetrodon* (Sphenacodontia, Pelycosauria) (Fig. 9), exhibit more circumscribed stresses, the latter are situated anteriorly (anterior position of stresses). Simultaneously, with this accumulation of vectors in *Dimetrodon*, there develop the posteriorly directed processes of the premaxillary bone which correspond to the frontal process of the premaxillary bone in mammals. The whole skull acquires the functional features with some similarity to the primitive breviarcuate skull. Accordingly the cranium of *Dimetrodon* is much more "cat like" than the skull of *Cynognathus* which rather resembles the transitory and primitive type of the insectivorous variant in the mammalian cranium.

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STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

IX. THE COMPARATIVE AND EVOLUTIONAL OUTLOOK

By R. Tucker*

(*Manuscript received June* 22, 1955)

Summary

In this paper an attempt is made to reach some general conclusions based on the descriptive, analytical, and comparative material gathered in Parts I-VIII of this series (Tucker 1954*a-f*, 1955*a*, *b*). The type of mastication is an important morphogenetical factor for all skulls with fixed (circumscribed) stresses. In the skull with dispersed stresses the morphogenetic influence of the splanchnocranium on the neurocranium is much smaller than in the skulls with fixed stresses. Consequently, the skulls with fixed stresses demonstrate typological, structural, and functional uniformity, while the development of neuro- and splanchnocrania in the skulls with dispersed stresses may follow various morphoevolutional directions.

The importance of this fact in the evolution of man is briefly discussed. The development of the human neurocranium is made possible by the technique of mastication, among other factors. The type of mastication practised is much less varied than the diet. Accordingly, it has much greater morphogenetical consequence.

It is suggested that the relations between environment and structure may occur only by means of function. Function influences the internal structure as well as affecting the environment. The morphofunctional influences of the type of mastication are discussed, using as an example the skulls of Lemuroidea. The functional analysis of the masticatory movements in *Smilodon* was used as an illustration of the transformative possibilities and their limitations connected with steno- and euryfunction. The stenofunctional animal can achieve morphological metamorphoses only through primary intraorganismic changes.

The formation and evolution of nodes from the primitive planoarcuate skull to the morphology of the breviarcuate, longoarcuate, and planoarcuate skulls are also demonstrated (cf. Table 1). The comparative morphology and topography of the supraorbital node, the fronto-premaxillary connections, the maxillary, and squamosal nodes as well as the interparieto-occipital node are given.

Relations to the craniological investigations of other workers are discussed.

I. The Splanchno-Neurocranial Relations

One of the general conclusions based on the analytical and comparative material of previous studies is the partial exemption of the neurocranium from close functional relationship with the splanchnocranium in all crania which demonstrate dispersed stresses. Another is the permanent and very strong morphofunctional and morphogenetic connections between the splanchnocranium and neurocranium in all skulls with circumscribed

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(fixed) stresses. The focusing of a force onto a relatively small area leads to the increase of stresses per unit area of surface. Accordingly, the stresses which reach a certain magnitude in relation to the circumscribed area are not opposed merely locally, but are transmitted and resisted by the whole cranial structure or by the greater part of it. Consequently, in the latter skulls, the way of intake and chewing of the food is an important morphogenic factor of the neurocranium. The results of it are demonstrated in the great typological and structural uniformity of the whole skull.

In the skulls with stresses which are not transmitted to distant points, the morphofunctional results are fairly varied. Both the neurocranium and the splanchnocranium may follow different morphotical and evolutional directions. In particular the neurocranium often develops ortho-evolutionally or under local stimulation (brain). Accordingly, the plano-arcuate skull is the skull of the most pronounced structural variety. Some examples of it are *Bathyopsis fissidens, Uintatherium laticeps, Arsinotherium zitteli, Ceratorhinchus, Coelodonta antiquitatis, Elephas primigenius,* recent and fossil man, as well as *Dinoceros mirabile* (Fig. 1). Similar transformative processes may be observed in reptilian skulls, whose structure really resembles the planoarcuate types of mammalian skull.

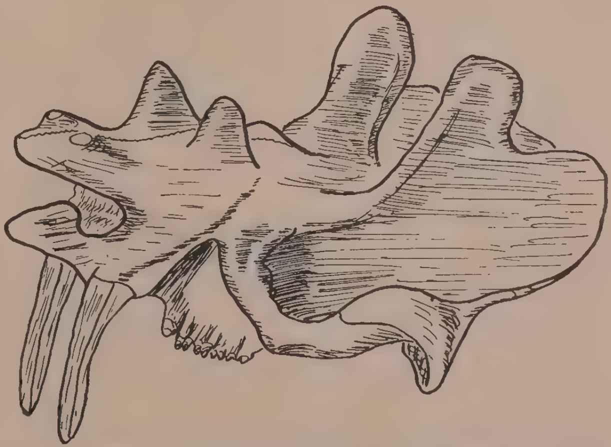


Fig. 1.—Skull of *Dinoceros mirabile* (from Nicholson (1879) after Marsh) (lateral view).

According to Murray (1954, personal communication) the real difference between the functional skull types is in the *intensity* of stresses per unit area of bone resistance. Hence (i) in skulls like the dog's, these stresses are of high intensity at the carnassial; (ii) in planoarcuate skulls the difference is that the stress of mastication is distributed over a larger area. This opinion is based on the postulate that when a force is applied to any solid body the stress is transmitted throughout it.

II. THE SKULL OF MAN AND ITS EVOLUTION

The relations between the neurocranium and splanchnocranium are also of importance in man. The skull of Hominidae is of the planoarcuate type. Accordingly, the neurocranium, largely freed from the morpho-functional connections with the splanchnocranium, may be shaped as a result of local factors which originate from the nervous tissue: for example, it may expand around an enlarged brain. In the longoarcuate and breviarcuate crania, the expansion of the neurocranial space is well nigh impossible, even from the purely mechanical aspect.

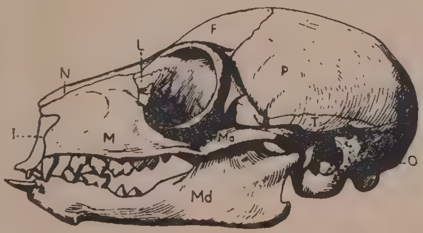
Hominidae were able to establish their position on the earth by the unique composition of various factors. Many of them have been discovered, investigated, and analysed. To my knowledge, the exemption of the human neurocranium from the splanchnocranial morphofunctional connections is not, up to date, considered as one of these factors. However, the development of the human brain is regulated, amongst other things, by the method of taking in food.

III. THE ECOLOGICAL APPROACH

Another rather general problem is raised by the ecological approach. The splanchnocranial relations to the neurocranium give evidence that the way in which the food is masticated, and the topography of the organs connected with the intake of the food, is even more important than the physical properties of different organic and nutritional materials. The longoarcuate skull is not the result of the hardness of the plant tissue. As a matter of fact, the food of many rodents is no harder than that of Equidae. The difference between the longoarcuate skull and the crania of the Hominidae, Suidae, or Pecora, considered even on the purely mechanical and functional basis, is not caused by the variation in the hardness of the food. On the other hand, the diet of many animals is varied to a much greater extent than is generally believed. The dog can live on rabbit meat but also on snails or baked potatoes. The cat eats rats but can survive on lizards and even cockroaches (Tucker, unpublished observations). In the wild state the variety of diet is greater and more unexpected. Most animals use a number of different foods (they are euryphagous) and only a few are bound to a particular kind of food (these are stenophagous). Foxes may be fruitivorous and insectivorous (Schoenichen 1938). Ruminants are sometimes carnivorous (Darling 1937), while bob-white quails (Leopold 1939) are reported to take in 927 different kinds of food.

Hediger (1950) surveyed the bibliography on the problems of euryphagy and stenophagy among animals. He stated that "among flesh and plant eaters, monotony of diet in the every-day meaning of the term is only to be found in books and zoological gardens. Too strong a warning cannot be given against over schematized classification of food based on tooth structure and theoretically co-ordinated diet".

Hence the method of crushing is more constant than the food crushed. The relations between environment and shape or between function and shape may give way to the chain formed by the successive environment-function-shape relations. The relationship of the environment to the function and that of function to the shape are direct, but the relationship between environment and shape is indirect. Environment and shape come together only through function. The environment may provoke the function, but cannot offer any definition of it. In other words, the environment touches only the periphery of the structure (in this case dentition) and affects its central or internal structures through function only. Function influences the deep structure as well as changing the environment.



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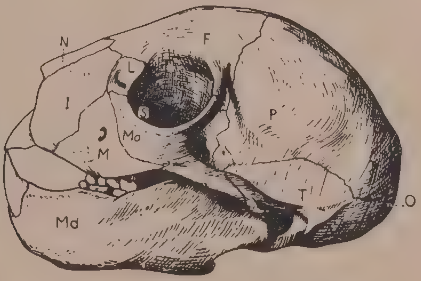

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Fig. 2.—Skull of *Lemur catta* (after Friant 1948) (by courtesy of Acta Anatomica).
Fig. 3.—The skull of *Chiromys madagascariensis* (after Friant 1948) (by courtesy of Acta Anatomica).

The deep transformations of the whole cranial structure caused by the above discussed relations are illustrated by the comparison of the crania of *Lemur catta* L. (Fig. 2) and *Chiromys madagascariensis* F. Geoffrey (Fig. 3). Both skulls belong to the Lemuroidea, and differ in the manner of food intake, *Lemur* being insectivorous with carnivorous tendencies, and *Chiromys* representing the trend to the longoarcuate (herbivorous) reconstruction. The typical transformations in *Chiromys* (Fig. 3) are demonstrated by:

(1) The enlargement of the premaxillary bone and creation of direct fronto-premaxillary connections (*Lemur catta* has fronto-maxillary connections);

(2) The high position of the nasal bones and their naso-premaxillary connections (in *L. catta* inferior position of the nasal bone and presence of naso-maxillary connections);

(3) The development of the adental margin and the transformation of maxilla (*L. catta* has an elongated alveolar process. The adental margin is not developed. The maxilla is elongated anteriorly);

(4) The anterior translocation of the zygomatic bone, the strong development of the zygo-lacrimal connections, and antero-dorsal translocation of the lacrimal bone (—the tendency to formation of the preorbital node);

(5) The slight weakening of the fronto-zygomatic connections;

(6) The low position of the zygomatic arch and loosening of its superior bending;

(7) The formation of the long principal arch of the cranium;

(8) The minimizing of the temporal (coronoid) process of the mandible;

(9) The increase of the height of the mandibular body and the development of the mandibular adental margin;

(10) The poor development of the horizontal lamina of the palatine bone.

Many similar transformations are dispersed throughout the whole cranial structure.

IV. The Problem of Morphological Transformations

The above discussed question of the crushing method of mastication can contribute to the problems of the external (ecological) and internal (enological) correlations. The functional analysis of the masticatory movements in *Smilodon* (Tucker 1954*e*) may be chosen as one example of this.

As a matter of fact, the stenophagy of *Smilodon* was purely mechanical. Accordingly, structure is affected by means of function (see above), the cat persistently using one function of many which it can perform. Thus its masticatory apparatus could specialize towards functional monotony. On the other hand, *Smilodon* could not do this simply because of the lack of a starting point from which to perform a modified function. Consequently, the function cannot develop in the organism and cannot influence deep structures. Hence environment can change the cat into *Smilodon* but cannot transform *Smilodon* into the cat. The morphological path from cat to *Smilodon* could be conditioned environmentally (ecologically), while the change from *Smilodon* to cat cannot occur. In other words, the cat is less specialized than *Smilodon,* and so could become specialized in any of a number of ways, one of which would lead to the *Smilodon* condition, whereas *Smilodon,* being already specialized, could only follow one line of evolution—that of the further development of its own specialization.

On the basis of these facts an animal can be considered as stenofunctional (able to perform one very limited and specialized function only) and euryfunctional (able to perform a number of similar functions). (I omitted the word "polyfunctional" for it can mean a number of functions of completely different character.)

V. The Comparative Analysis

The functional analysis of the mammalian skull touches evolutional as well as systematical problems. Starting with the primitive planoarcuate type, as seen in mesozoic mammals, and using the comparative method, it is possible to trace the morphofunctional transformations of the skull.

The primitive supraorbital node is simple. The breviarcuate and planoarcuate skulls evolved towards the development of the strong connections with the malar bone, and the zygomatic arch. The full development of these connections—direct bony contact—is present in the planoarcuate skull. In consequence, the frontal bone has an inelastic burden and the zygomatic arch is shortened. In the breviarcuate skull these connections are elastic and the zygomatic arch is distinctly bent. In the longoarcuate skull the functions of the supraorbital node are taken over by the preorbital node. The latter results in the elongation of the zygomatic arch and its inferior bending (towards the alveolar process).

The fronto-zygomatic connections in different types of skull are summarized in Table 1.

Table 1

RELATIONSHIPS BETWEEN PRIMITIVE PLANOARCUATE, PLANOARCUATE, BREVIARCUATE, AND LONGOARCUATE SKULLS

Skull Part	Primitive Planoarcuate	Planoarcuate	Breviarcuate	Longoarcuate
Supraorbital node	Simple	Well developed	Distinctly developed	Absent
Postorbital process	Only just evident	Well developed, reaching malar bone	Well developed	Connections of frontal bone with zygomatic arch partially or completely through lacrimal bone
Connections:				
Malar bone	None	—	Elastic	—
Fronto-zygomatic	—	Direct and non-elastic	—	Non-elastic, possibly indirect
Zygomatic arch	Poorly developed,* situated horizontally	Medium development, short, situated horizontally	Very well developed, bent superiorly	Very well developed, reaches max. length, bent inferiorly

* Or even only partially developed.

VI. THE PREMAXILLARY NODE

The premaxillary node is very well developed in the longoarcuate skull, distinct in the breviarcuate skull, of slight development in the primitive planoarcuate skull, and undeveloped in the more advanced planoarcuate skull. Accordingly, the relations of the premaxillary bone to the other components of the skull differ in the various functional types. The direct fronto-premaxillary connections are present only in the longoarcuate skull. In the breviarcuate type, the maxilla contacts the frontal bone, and in the planoarcuate skull, the lacrimal bone penetrates between the maxilla and frontal bone. In the longoarcuate skull, the maxilla contacts the nasal bone. These points may be summarized as follows: Fronto-premaxillary connections are present in the longoarcuate skull, but absent in breviarcuate, planoarcuate, and primitive planoarcuate skulls.

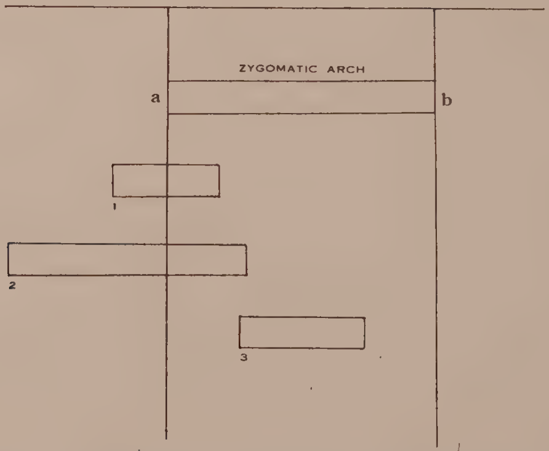

Fig. 4.—Position of the maxillary node in relation to the zygomatic arch. *a*, The anterior end of the zygomatic arch; *b*, the posterior end of the zygomatic arch. *1*, Position of the maxillary node in the breviarcuate skull. *2*, Position of the maxillary node in the planoarcuate skull. *3*, Position of the maxillary node in the longoarcuate skull.

VII. THE POSITION OF THE MAXILLARY NODE

The maxillary node is very stable and displays only two variations in shape (i) short, (ii) elongated. The first variation demonstrates the maxillary node of the skull with fixed stresses, and is present only in the breviarcuate type. The maxillary node shaped in this way is always situated at the anterior end of the zygomatic arch, while the node of the planoarcuate and longoarcuate types usually occupies a larger area and comprises a more elongated structure. In the planoarcuate type, the greater part of it is placed anteriorly to the zygomatic arch. In the longoarcuate skull, the maxillary node is translocated caudally to the zygomatic arch. In this skull the whole alveolar process occupies the place between the ends of the zygomatic arch (Fig. 4).

VIII. The Translocations of the Squamosal Node

The squamosal node is translocated anteriorly and superiorly in the longoarcuate skull, according to the general anterior tendency of this type most distinctly demonstrated in the development of the premaxillary node. The anterior and superior position of the squamosal node in this skull results in the weakening of the squamoso-occipital connections. The migration of the squamosal node, the absence of the supraorbital node, and the creation of the more anteriorly situated preorbital node together with the specific development of the premaxillary node, completely destroy the regular tri-triangular plan of the breviarcuate type.

IX. The Interparieto-Occipital Node

The interparieto-occipital node is the only (median) node in the breviarcuate skull. In this node both morphofunctional antimers are really bound together. The position of the interparieto-occipital node in the planoarcuate and longoarcuate skulls is changed, and the node itself is transformed as a result of:

(1) The anterior migration of the squamosal node;

(2) The anterior translocation of the masseter; and

(3) The decrease in importance of the squamosal muscle in the mechanism of the quick movement of the mandible.

X. The Mechanics of the Mandible

The transformations of the squamosal node and the masseter are demonstrated particularly well in the longoarcuate type. In the longoarcuate as well as in the planoarcuate skull, the speed of the mandibular movements decreases simultaneously with the changes in the temporal muscle. The shape of the interparieto-occipital node in the breviarcuate skull provides more evidence of speed on the level of the premaxillary bone, and the speed of the mandibular movements is of great importance for these animals of prey. It is much less important for the herbivores which feed on non-motile, but often very hard, food. The development of the premaxillary node, the elongation of the principal arch of the cranium, the anterior migration of the masseter, and the developmental topographic relations of the temporal muscle are closely bound with one another and have their specific morphofunctional significance in the longoarcuate skull. In a similar way, the topography of the masseter, the fronto-zygomatic connections, and the shaping of the maxillary node are significant and characteristic of the planoarcuate skull.

XI. Discussion

Recently, three craniological papers were published dealing with functional and analytical investigations. These are by Barnikol (1952) describing the correlations in the process of formation of the avian cranium, Schuchardt (1952) on the growth relations between the brain and the mammalian cranium, and Wimmer (1953) on the architecture of the sinus sagittalis cranialis.

Barnikol (1952) made a detailed comparative study of the reciprocal relations and influences between various elements of the avian skull, and in particular studied the masticatory musculature, cranial nerves I, II, III, IV, V_1, V_2, V_3, VI, and VII, the processes, ligaments, glands, and vessels. He investigated 43 various species among the Sphenisci, Steganopodes, Ciconiae, Anseres, Cathartae, Accipitres, Galli, Oposthocomi, Limicolae, Lari, Columbae, Cuculi, Coraciae, Striges, Cypseli, Pici, and Passeres (Gadow's system (1891-3)). He gives also an extensive survey of the literature.

Wimmer (1953) studied the functional connections and adaptations of the dura mater cranialis, concentrating on the microscopical study in the surroundings of sinus sagittalis cranialis.

Schuchardt (1952) investigated crania of cattle, cats, guinea pigs, and men by means of measurements and indices, mainly tracing the relations between the basis of the cranium and the length of the skull. The investigations of Barnikol (1952) led him, among other things, to the phylogenetical conclusions which give a striking similarity to the comparative results presented above, and reached independently by me on quite different craniological material. Barnikol expresses the opinion that the original form of avian skull is a "stretched one".

Wimmer (1953) found that the connective tissue formations in organs are shaped according to the mechanical factors which influence the tissue in a very complicated way. Only in the light of "statico-dynamic" reality he sees the sense of morphological discoveries and the possibility of investigating the physiological and pathological phenomena. Schuchardt (1952) applying mathematical methods, approaches the onto- and phylogenetic problems, the genomorphological relations, and the possibility of investigations of quantitative craniological changes.

The relations of the conclusions of Barnikol (1952), Schuchardt (1952), and Wimmer (1953) to the results of my own investigations are apparent. The differences in material, methods, and the summarizing of results are about as great as they could be; however, they are complementary in that they focus the investigations on the same problems. On the other hand, the manner of transformations of nodes and tracts in the orbito-squamosal regions throws some light onto the observations of de Beer (1928) who found that the side wall of the vertebrate skull has been expanded independently several times. In each case the original wall disappears at least in part.

Dentition as the morphogenetical factor in the development of the splanchnocranium has been included several times in craniological theories. The origin of the bones surrounding the buccal cavity in vertebrates was explained by Hartwig (1874) by means of the concrescence of the bases of the teeth. This interpretation was disproved, however, by Goodrich (1903, 1907) and Sewertzoff (1926). Gaupp (1901) cautiously suggested that there may be a connection between the development of the bones of the splanchnocranium and the presence of teeth. It is possible to interpret his approach as functional in type. However, the general statements of the functional relations between topographically connected parts of an organism are not rare.

The conclusions from present investigations differ from the conclusions and suggestions of the authors mentioned above in that the dentition does not form the only keys to understanding the splanchnocranium and is not a separate and powerful creation centre, but is an object of morphogenetic influences which are fairly uniform in the whole cranial system. Accordingly, the morphofunctional relations in the splanchno- and neurocranium do not form two separate groups and their morphogenetic value is not limited or extended by its topographical relations only.

Finally, an attempt is made to study the methods and scope of these relations.

XII. ACKNOWLEDGMENT

My thanks are due to the publishers of Acta Anatomica for permission to reproduce the skulls of *Lemur catta* and *Chiromys madagascariensis*.

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STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

X. THE DENSITY OF THE BONY TISSUE IN NODES AND TRACTS

By R. TUCKER*

(*Manuscript received June* 22, 1955)

Summary

The skulls of the dog, cat, foetal horse, and *Echidna* were investigated by means of X-rays with regard to the bone density in various regions. The marked increase in the density of the bony tissue around the nodes and along the tracts was observed. The tracts and nodes were analysed and described in previous papers (cf. Parts I-IX of this series (Tucker 1954*a-f*, 1955*a-c*)). As the nodes and tracts are the paths of stresses, the increased density of the bony tissue in them is interpreted functionally; it increases, namely, the resistance of the whole structure to the stresses which originate from mastication.

Other areas of high density of bony tissue are located around the foramen magnum and in the petrosal bone. The first is connected with the stresses which originate from the vertebral column and the mass of the whole head as well; the second is related to the development of the internal ear.

I. INTRODUCTION

The nodes and tracts of the planoarcuate, breviarcuate, and longoarcuate skulls discussed in previous papers (Parts I-IX of this series (Tucker 1954*a-f*, 1955*a-c*)) are accentuated by many external morphotic features. Those external expressions of nodes and tracts open the problem of the internal characteristics of the bony tissue in them. The latter problem leads in turn to the broader question of the distribution of the bony tissue within the skull. It seems quite reasonable to assume that in the mechanically important regions the disposition of stresses can be facilitated by the increased density of the bony tissue. Accordingly these relations were investigated by means of X-rays. The main subject of the study now presented is the breviarcuate skull. This skull was chosen deliberately as a distinctly hypöostotic type (Parts III-VI, VIII, IX) with well-developed transmissive structures (Parts I-IX).

II. THE DEMONSTRATION OF BONE DENSITY

When the body is X-rayed, the areas of higher density of tissue appear lighter than the areas of low density. Accordingly, various shades from deep black to completely white, seen on the photographs, correspond to the various degrees of density of the tissues. Because the whole series of the functional and analytical studies (Parts I-IX) is concerned with the stresses in the cranial bones, dry skulls only were used for all investiga-

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tions in this study. On the other hand, this eliminates the shadows which can be caused by other tissues.

The white areas on the X-ray photographs of the skull are caused by:

(1) The increased density of the bony tissue;

(2) The increased thickness of the bony structure.

Both these alternatives give better resistance to the cranial structure previously discussed (see Parts I-IX).

Plate 1, Figure 1, shows the X-ray photograph of the squamosal bone of the *Echidna*. The skull of the *Echidna* is largely exempted from masticatory stresses and accordingly its squamosal bone *a* is very thin. There are only a few distinctly developed ridges present around the squamosal node *b*. The thinness of the squama proper in the *Echidna* is demonstrated by comparison with the block of high density formed by the petrosal bone *c*.

The density of the bone of the splanchnocranium, which does not develop great stresses for masticatory movements, is shown in Plate 1, Figure 2, where the maxilla *b* and premaxilla *a* of the *Echidna* are illustrated. However, the increased density is visible in the premaxillo-supraorbital tract *c*.

The formation of tracts and nodes occurs during the embryonal period. Its external development is paralleled by the changes in the density of the bony tissue in tracts and nodes. Plate 1, Figure 3, shows the right frontal bone of the horse foetus, aged about 8 months. The supraorbital node *b* has already a very dense composition when compared with the rest of the frontal bone *a*. The postorbital process *c* also shows marked density of the bone.

III. BONE DENSITY IN TRACTS AND NODES OF THE SKULL OF THE CAT

In the X-rayed skull (in the dorso-ventral direction) of the cat (Plate 1, Fig. 4), a high degree of bone density is visible in the premaxillo-maxillary tract *a*, supraorbito-maxillary tract *b*, supra-orbito-squamosal tract *c*, interparieto-occipito-squamosal tract *d*, and maxillo-squamosal tract *e*. Furthermore, the marked increase of density of the bony tissue is accentuated in the zygo-sphenoidal curvature *f* (Tucker 1954*c*), intermaxillary suture *g*, in which powerful transverse stresses act (Tucker 1954*c*), squamosal node *h*, interparieto-occipital node *i*, petrosal bone *j*, and premaxillary node *k*. The maxillary node is represented by the size and high tissue density of the carnassal *l*.

The distribution of the dense bony tissue within the skull shows that the density of the bony tissue in all tracts and nodes is increased in relation to the other areas of the skull except the petrosal bone and condyli (see below). Thin structures of dense bony tissue are also visible in the frontal process of the malar bone *m* and in the post-orbital process of the frontal bone *n*. Markedly light spots *o* are visible around the canine.

IV. Bone Density in the Tracts and Nodes of the Dog

The distribution of bony density in the right- and left-half of the skull of a $2\frac{1}{2}$-year old greyhound are shown in Plate 1, Figure 5, and Plate 2, Figure 6. Plate 1, Figure 5, shows the lateral side of the skull together with the zygomatic arch. The zygomatic arch *a*, premaxillo-maxillary tract *b*, maxillo-squamosal tract *c*, squamosal node *d*, interparieto-occipito-squamosal tract *e*, interparieto-occipital node *f*, interparieto-occipito-supraorbital tract *g*, supraorbito-maxillary tract *i* are clearly accentuated.

The tracts and nodes are equally easily demonstrated when the zygomatic arch is removed (see Plate 2, Fig. 6). The three triangles *A*, *B*, *C* are distinctly outlined (cf. Tucker 1954*c*). The supraorbito-squamosal tract *a*, premaxillo-supraorbital tract *b*, supraorbital node *c*, interparieto-occipital-supraorbital tract *d*, the roof of the frontal sinus *e*, maxillary node *f*, premaxillo-maxillary tract *g*, maxillo-squamosal tract *h*, and squamosal node *k* are clearly distinguished by the density of the bony tissue in them. The bone density in the occipital region of the dog (see Plate 2, Fig. 7) is highest around the occipital foramen *a* and at the occipital condyli *b*. The high density of those structures is not connected with masticatory stresses. Other dense parts are the interparieto-occipital node *c* and the interparieto-occipito-squamosal tract *d*. Plate 2, Figure 8, shows the isolated parietal bone of the dog. The densest areas appear to be in the interparieto-occipito-supraorbital tract *a* and interparieto-occipito-squamosal tract *b*.

Plate 2, Figure 9, shows the anterior triangle of a young dog during the change of dentition. Clearly indicated are dense areas in the premaxillo-maxillary tract *a*, around the premaxillary node *b*, around the maxillary node *c*, and in the premaxillo-supraorbital node *d*.

The distribution of the dense bony tissue in the area of the supraorbital node of the dog is shown in Plate 2, Figure 10. The dense areas are visible in the frontal bone *c* (roof of the frontal sinus), in the premaxillo-supraorbital tract *d*, in the interparieto-occipito-supraorbital tract *f*, and in the supraorbito-squamosal tract *g*.

V. Discussion

The existence of the nodes and tracts are demonstrated by means of the bone density within the skull. The areas of high bone density correspond to the previously described and demonstrated tracts and nodes in the skull which were analysed morphologically (see Parts I-IX). Accordingly they should have mechanical significance, and most of them, with the exception of the petrosal bone and the surroundings of the foramen occipitale magnum, are connected with the stresses which originate from masticatory functions.

VI. ACKNOWLEDGMENT

I wish to thank Mr. S. Gould for technical assistance.

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Fig. 1.—Squamosal and petrosal bones of *Echidna*. *a*, Squama of the squamosal bone; *b*, squamosal node; *c*, petrosal bone; *d*, anterior part of squamosal bone; *e*, posterior part of squamosal bone.

Fig. 2.—Premaxillo-supraorbital tract in *Echidna*. *a*, Premaxillary bone; *b*, maxilla; *c*, premaxillo-supraorbital tract.

Fig. 3.—The right frontal bone of the horse foetus (about 8 months old). *a*, Frontal bone; *b*, supraorbital node; *c*, postorbital process; *d*, supraorbital foramen; *e*, frontal sinus; *f*, posterior part; *g*, anterior part.

Fig. 4.—The density of bony tissue in the skull of the adult cat. X-ray photograph, dorso-ventral position. Right malar bone removed. *a*, Premaxillo-maxillary tract; *b*, supraorbito-maxillary tract; *c*, supraorbito-squamosal tract; *d*, interparieto-occipito-squamosal tract; *e*, maxillo-squamosal tract; *f*, zygo-sphenoidal curvature; *g*, intermaxillary suture; *h*, squamosal node; *i*, interparieto-occipital node; *j*, petrosal bone; *k*, premaxillary node; *l*, carnassal; *m*, malar bone; *n*, postorbital process of the frontal bone; *o*, canine alveolus.

Fig. 5.—X-ray photograph of tracts and nodes in the skull of the 2½-year old greyhound. Right side. Premaxillary bone removed. *a*, Zygomatic arch; *b*, premaxillo-maxillary tract; *c*, maxillo-squamosal tract; *d*, squamosal node; *e*, interparieto-occipito-squamosal tract; *f*, interparieto-occipital node; *g*, interparieto-occipito-supraorbital tract; *i*, supraorbito-maxillary tract; *j*, frontal sinus.

PLATE 2

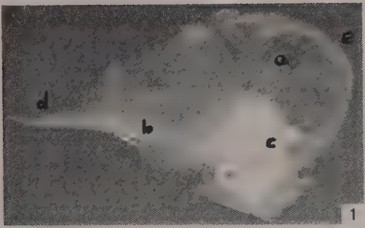
Fig. 6.—X-ray photograph of tract and nodes in the skull of the 2½-year old greyhound. Left side. Zygomatic arch, occipital, and interparietal bones removed. *A*, Anterior triangle; *B*, middle triangle; *C*, posterior triangle; *a*, supraorbito-squamosal tract; *b*, premaxillo-supraorbital tract; *c*, supraorbital node; *d*, interparieto-occipito-supraorbital tract; *e*, frontal bone (roof of the frontal sinus); *f*, maxillary node; *g*, premaxillo-maxillary tract; *h*, maxillo-squamosal tract; *k*, squamosal node.

Fig. 7.—X-ray photograph of the occipital and interparietal bones of a middle-sized dog (mongrel). *a*, Foramen occipitale magnum; *b*, condyli; *c*, interparieto-occipital node; *d*, interparieto-occipito-squamosal tract.

Fig. 8.—X-ray photograph of the parietal bone (left) of a middle-sized dog (mongrel). *a*, Interparieto-occipito-supraorbital tract; *b*, interparieto-occipito-squamosal tract; *c*, anterior part; *d*, posterior part.

Fig. 9.—X-ray of the anterior triangle of a young dog. *a*, Premaxillo-maxillary tract; *b*, dense tissue around the premaxillary node; *c*, dense tissue around the maxillary node; *d*, premaxillo-supraorbital node.

Fig. 10.—Density of the bone in the supraorbital node of a dog. *a*, Posterior part; *b*, anterior part; *c*, roof of the frontal sinus; *d*, premaxillo-supraorbital tract; *e*, frontal sinus; *f*, interparieto-supraorbital tract; *g*, supraorbito-squamosal tract.



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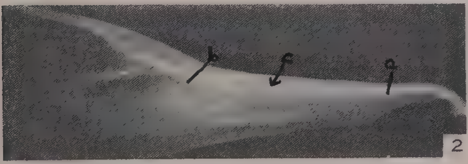

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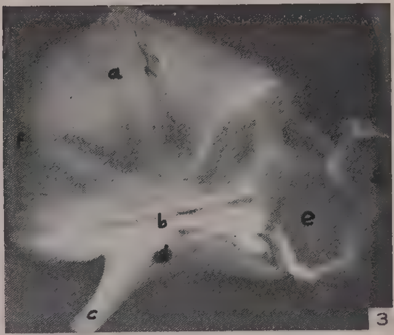

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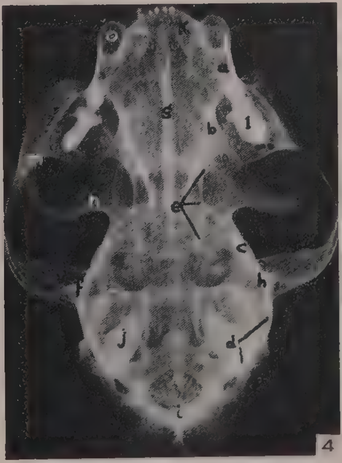

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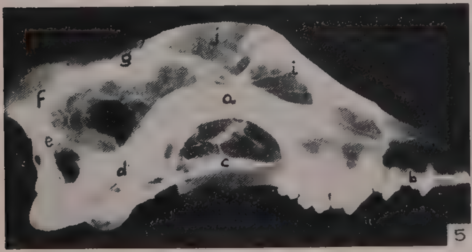

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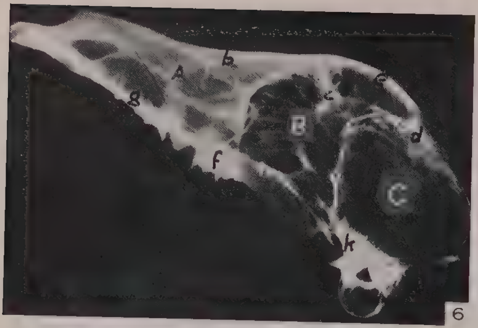
FUNCTIONAL AND ANALYTICAL CRANIOLOGY. X



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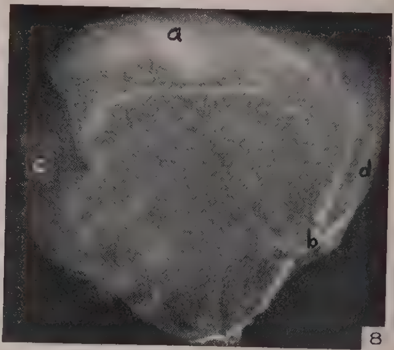

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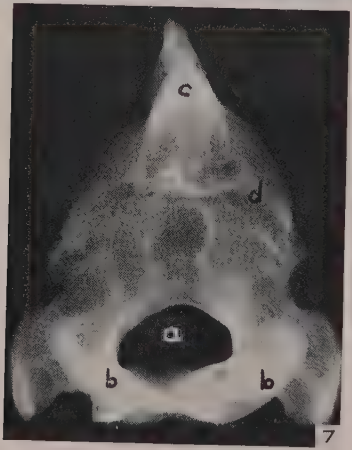

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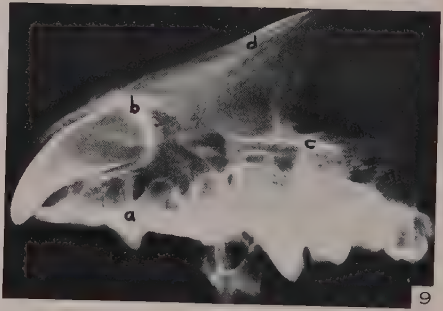

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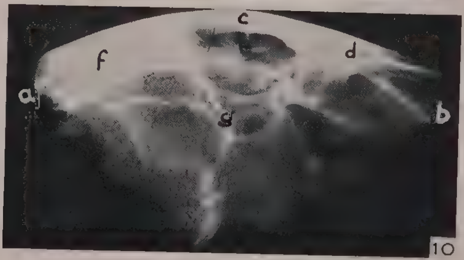

10

THE GENUS DROSOPHILA (DIPTERA) IN EASTERN QUEENSLAND

I. TAXONOMY

By W. B. Mather*

(*Manuscript received November 29, 1954*)

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Summary

Ten species of which six are new, of the genus *Drosophila* are described and figured: *D. cancellata*, sp. nov., *D. enigma* Mall., *D. lativittata* Mall., *D. opaca*, sp. nov., *D. maculosa*, sp. nov., *D. levis*, sp. nov., *D. serrata* Mall., *D. takahashii* Sturt., *D. dispar*, sp. nov., and *D. versicolor*, sp. nov. Laboratory cultures of these have been set up from single females fertilized in the wild, allowing descriptions of eggs, larvae, pupae, and certain internal structures and external anatomy of the adults. These species have been assigned to subgenera and species group and their geographical distribution is recorded, together with the known Queensland distribution of *D. busckii* Coq., *D. melanogaster* Meig., *D. simulans* Sturt., *D. ananassae* Dol., *D. hydei* Sturt., *D. repleta* Woll., *D. immigrans* Sturt., and *D. spinofemora* Patt. & Wheel. These 18 species are keyed. The taxonomy of the subgenus *Pholadoris* is discussed, and three new species groups established, namely, *coracina*, *maculosa*, and *levis*. A new species group within the subgenus *Sophophora*, namely, *dispar*, is established.

I. Introduction

The only published work on the genus *Drosophila* in Australia has been by Duda (1923) and by Malloch (1923, 1924, 1925, 1927). Duda described three indigenous species, and Malloch 18. Malloch also recorded

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five cosmopolitan species: *D. busckii* Coq., *D. hydei* Sturt., *D. immigrans* Sturt.,* *D. melanogaster* Meig., and *D. repleta* Woll.

Prior to this study only two species, *D. serrata* Mall. and *D. albostriata* Mall., had been recorded from Queensland. The present study is the result of collections made in Queensland, particularly in the south-east corner of the State over the past 3 years (Table 8 and Fig. 1).

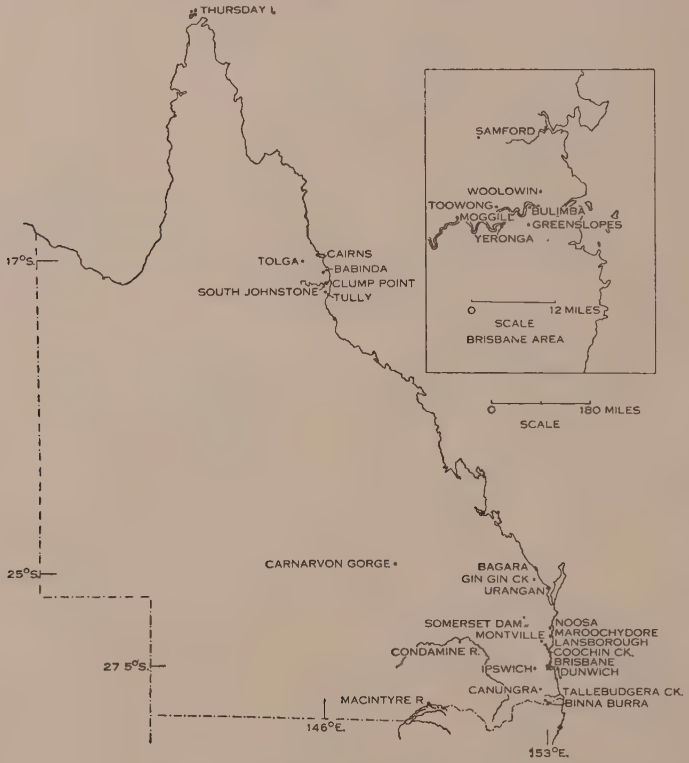

Fig. 1.—Distribution of *Drosophila* in Queensland.

II. TYPE MATERIAL

Malloch's types, which have been examined by the author are located as follows: (i) Australian Museum, Sydney: *D. albostriata*, *D. brunneipennis*, *D. inornata*, *D. lativittata*, *D. mycetophaga*, *D. obsoleta*, *D. polypori*, and *D. setifemur*; (ii) School of Public Health and Tropical Medicine, University of Sydney: *D. enigma*, *D. fuscithorax*, *D. nicholsoni*, *D.*

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* The specific name *D. immigrans* has been retained for this species pending a ruling from The International Commission on Zoological Nomenclature on the application put forward by Mayr, E., Patterson, J. T., Wheeler, M. P., and Spencer, W. P. (1954).—*Bull. Zool. Nomencl.* 9: 161.

nigrovittata, *D. poecilithorax*, *D. serrata*, *D. subnitida*, and *D. sydneyensis*. The location of Malloch's type *D. flavohirta* is unknown, but Lee (personal communication) states that "the U.S. National Museum possesses six paratypes". Duda's types of *D. australica*, *D. biradiata*, and *D. interrupta* are in the Budapest Museum.

Two paratypes of each sex of species, here described as new, and two plesiotypes of redescribed species have been deposited as pinned material at the Australian Museum, Sydney; British Museum; U.S. National Museum; Division of Entomology, C.S.I.R.O., Canberra, A.C.T.; Queensland Museum; and the School of Public Health and Tropical Medicine, University of Sydney. The ♂ holotype and allotype of each new species have been deposited at the Australian Museum. In addition, slides of the hypopygium of all species described have been deposited at the above institutions. This procedure has been adopted, due to the confusion caused in the past by type material consisting only of pinned specimens. These types and the above deposited material have been taken from type cultures, which are maintained at the Zoology Department, University of Queensland, Brisbane, and are descended from single females fertilized in the wild.

III. TECHNIQUES

The material studied was collected by Patterson's (1943) method and type cultures maintained by Spencer's (1950) standard method.

In general, descriptions are based on single adult specimens taken from the type culture. For the following characters, 10 specimens of each sex were measured: arista branches, cheek-eye ratios, sterno-indices, body lengths, wing lengths, and wing indices. In the case of pupae the number of branches of the anterior spiracles, the stalk length in relation to pupal length, and the relationship of the posterior spiracles to one another have also been determined from 10 individuals. For species within the subgenus *Pholadoris*, egg filament number has been determined from 50 eggs, taken from a mass culture.

Wings, external genitalia, and legs have been mounted in Womersley's (1939) medium. Drawings were made on graph paper using a squared eyepiece. Dissections were made in 0.7 per cent. saline, and colours expressed by the Maertz and Paul (1950) standard scale.

Measurements were made by a micrometer eyepiece. Body length is here taken as the distance from the posterior extremity of the fly to the most anterior point of the abdomen, plus the distance from here to the antennal base, both measurements being made laterally (Fig. 2*B*). Body length is split into two components because of the variable flexure at the abdominal-thoracic junction. Measurements have been made on freshly killed flies to obviate inaccuracies due to shrinkage.

Wing length is here taken as the distance from the more basal division of the common trunk of the 1st, 2nd, and 3rd longitudinal veins to the

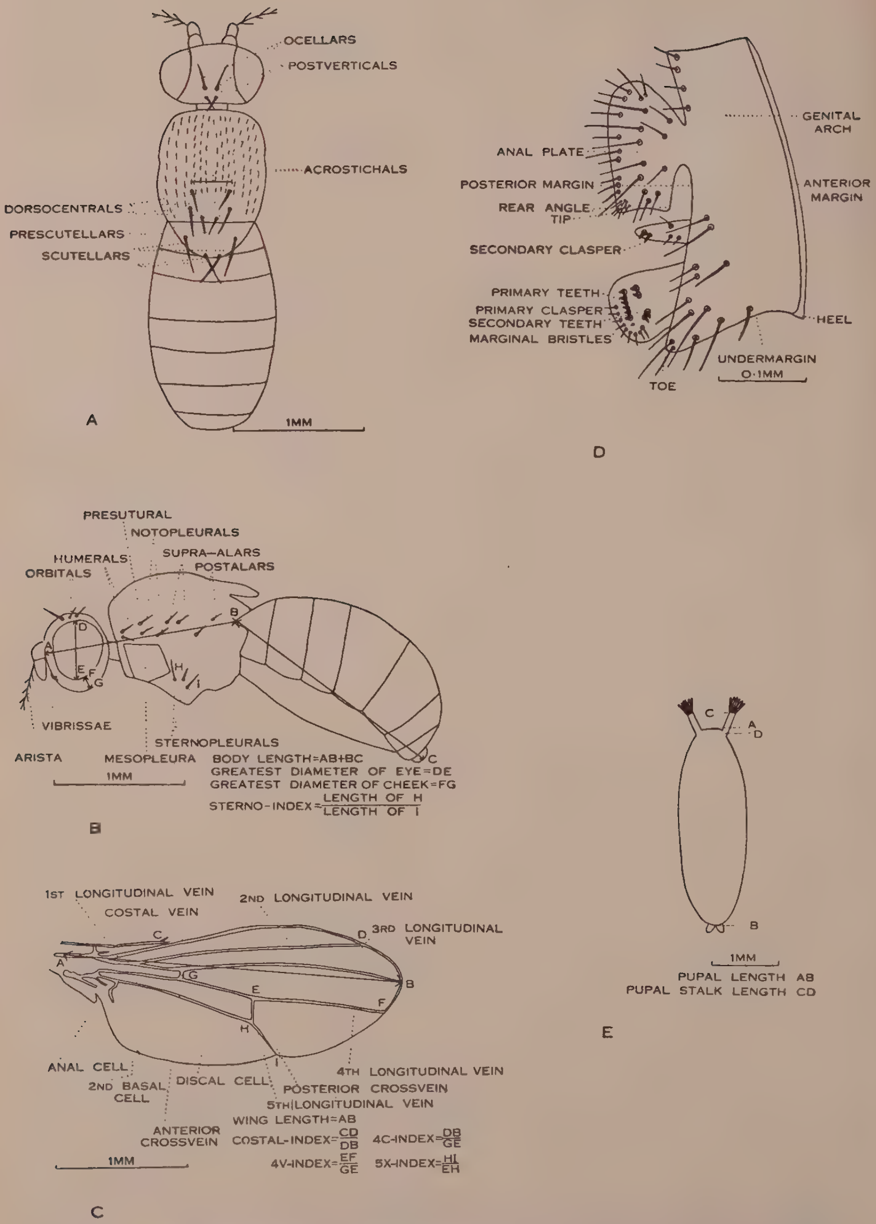

Fig. 2 *A-F*.—Hypothetical Drosophila showing features of taxonomic importance: *A*, dorsal view — wings and legs removed; *B*, lateral view — wings and legs removed; *C*, wing; *D*, hypopygium (after Hsu 1949); *E*, pupa.

intersection of the costal and 3rd longitudinal veins (Fig. 2*C*). These reference points were chosen as being the most practicable identifiable points approximating to the actual length of the wing.

Pupal stalk length is here defined as the length of the stalk of the anterior spiracles, and pupal body length as the length of the pupa excluding both the anterior spiracles together with their stalks and the posterior spiracles (Fig. 2*E*). These measurements have been chosen, because with them a high degree of accuracy is possible, whereas this is not the case with the "horn index".

The abundance of each species in a catch is expressed as two fractions (the female being listed first), except for the massive catches from the University Farm, Moggill, Brisbane, which will be detailed in a later paper. The females of certain species are most difficult to distinguish externally and this is indicated by a query (?).

Standard technical terminology (Sturtevant 1921, 1942) and the special terminology developed for the ♂ external genitalia (Hsu 1949) are followed (Fig. 2).

KEY TO THE QUEENSLAND SPECIES OF THE GENUS DROSOPHILA

1.	Prescutellar bristles present	2
	Prescutellar bristles absent	5
2 (1).	Thorax of uniform colour	3
	Thorax not of uniform colour	4
3 (2).	Thorax brown	*levis*, sp. nov.
	Thorax black	*opaca*, sp. nov.
4 (2).	Thorax with white streak between the 2 median rows of acrostichals (Fig. 5*A*)	*lativittata* Mall.
	Thorax with white streak between the 2 submedian rows of acrostichals (Fig. 4*A*)	*enigma* Mall.
	Thorax with 2 submedian rows of 3 white spots (Fig. 7*A*)	*maculosa*, sp. nov.
	Thorax with 2 submedian white stripes on anterior part (Fig. 3*A*)	*cancellata*, sp. nov.
5 (1).	Thorax striped	*busckii* Coq.
	Thorax not striped	6
6 (5).	Thorax with bristles arising from black spots	7
	Thorax not spotted	9
7 (6).	Lateral abdominal yellow spots (Fig. 12*A*)	8
	No lateral abdominal yellow spots	*hydei* Sturt.
8 (7).	Testes white*	*repleta* Woll.
	Testes orange*	*versicolor*, sp. nov.
9 (6).	A comb-like series of stout bristles on femur of 1st leg	10
	No comb-like series of stout bristles on femur of 1st leg	11
10 (9).	Eyes red and 3rd costal section with heavy bristles on its basal quarter	*immigrans* Sturt.
	Eyes orange and 3rd costal section with heavy bristles on its basal half	*spinofemora* Patt. & Wheel.

* Testes colour may be determined in the intact fly as the ventral abdominal wall is translucent.

Males Only

11 (9). **Sex comb absent** .... ***dispar*, sp. nov.**
Sex comb present **12**

12(11). **Longitudinal sex comb** **13**
Transverse sex comb **15**

13(12). Longitudinal sex comb on 1st and 2nd tarsal segments of 1st leg (Fig. 9*A*) .... ***serrata* Mall.**
Longitudinal sex comb on distal half of 1st tarsal segment of 1st leg 14

14(13). Posterior margin of genital arch very conspicuous and clam-shaped .... ***simulans* Sturt.**
Posterior margin of genital arch inconspicuous ....*melanogaster* Meig.

15(12). Transverse sex comb on 1st leg; 6 rows on 1st tarsal segment, distal 2 prominent; 2 rows on 2nd tarsal segment, prominent (Fig. 10*C*) .... ***takahashii* Sturt.**
Transverse sex combs on 1st leg; 2 rows on 1st tarsal segment and 1 on 2nd tarsal segment .... ***ananassae* Dol.**

IV. Species Descriptions

Genus DROSOPHILA Fallén

Drosophila Fallén, 1823, Diptera Sueciae Geomyzides. Part 2: p. 4.

Subgenus PHOLADORIS Sturtevant

***Pholadoris* Sturtevant, 1942, Univ. Tex. Publ. 4213: 28.**

Species group CORACINA, sp. gr. nov.

Black or brown species, anterior scutellar bristles divergent, acrostichal hairs in 8 rows, cheeks 0.2 width of eyes. Male genitalia with squarish heel to genital arch, the latter lightly bristled below; anal plate with not especially dense bristles at lower tip; clasper without numerous fine hairs, and not extended outward beyond primary teeth. Posterior malpighian tubules with common trunk 0.1-0.3 their total length. Larvae white in colour, ventral hooklets yellow, larval salivary glands of equal size. Egg filaments showing both intraspecific and interspecific variability and lying in the range of 4-10.

Drosophila cancellata, sp. nov.

Fig. 3*A-D*

General: Black thorax with 2 submedian white streaks anteriorly (Fig. 3*A*).

Description

Type Culture Source.—Moggill, 19.xi.1952 (Fig. 1).

Body Length.—♂ 2.8 mm, ♀ 3.0 mm.

Head ♂ and ♀.—Arista with 6-8 branches. Orbital bristles in the ratio of about 2 : 1 : 2. Second oral bristle about 0.3 of 1st. Greatest width of cheeks 0.2 greatest diameter of eyes. Eye colour red (6L9). Carina flat.

Thorax ♂ and ♀.—Black, with 2 submedian white streaks anteriorly (Fig. 3*A*). Acrostichal hairs in 8 rows. Prescutellars present. Anterior scutellars divergent. Sterno-index 0.8. Apical bristles on 1st and 2nd tibia, preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Clouding over crossveins. Costal index 2.4, 4th vein index 2.2, 5x index 1.3, 4c index 1.2. Third costal section with heavy spines on its basal 0.6. Length: ♂ 2.5 mm, ♀ 2.6 mm.

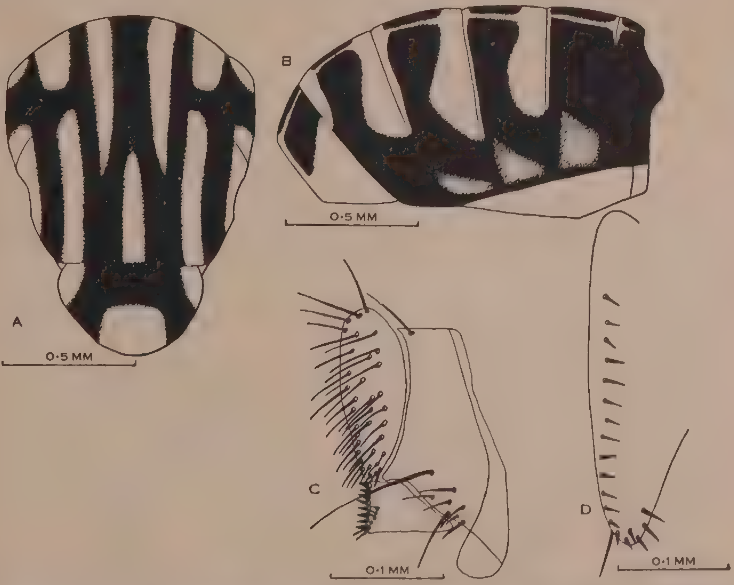

Fig. 3 *A-D.*—*D. cancellata*: *A*, ♂ thorax, dorsal view; *B*, ♂ abdomen, dorsolateral view; *C*, hypopygium; *D*, ovipositor plate.

Abdomen ♂.—First segment black, interrupted dorsally with yellow. Second segment similar, but with ventrolateral yellow patch. Third and 4th segments with black band posteriorly, interrupted dorsally with yellow and with ventrolateral yellow patches. Fifth segment with black band posteriorly, interrupted dorsally with yellow. Sixth segment black dorsally, interrupted with yellow (Fig. 3*B*).

♀.—Similar to ♂ but with 6th segment similar to 5th, and 7th segment all black.

External Genitalia.—♂. Genital arch broad in centre, about 1 bristle on upper margin, about 8 bristles below, heel round, undermargin straight, toe pointed and above level of heel. Anal plate oval, free, about 35 bristles evenly distributed, rear angle absent. Primary clasper free, about 2 marginal bristles posteriorly, about 8 primary teeth in straight row, about 5 bristles posteriorly. Secondary clasper absent (Fig. 3*C*).

SUBGENUS PHOLADORIS: EXTERNALS

TABLE 1

D, divergent; *C*, convergent; *T*, transparent; *C/C*, clouded over crossveins

Species Group and Spp.	Orbital Bristles Ratio	Arista Branches	Oral Bristles Ratio	Cheek-Eye Ratio	Rows of Acrostichals	Anterior Scutellars	Sterno-index	Wing Colour	Costal Index	4th Vein Index	5x Index	4c Index	3rd Costal Section Ratio	Wing Length ♂ (mm)	Wing Length ♀ (mm)	Body Length ♂ (mm)	Body Length ♀ (mm)
victoria																	
*lebanonensis**	4:1:4	7	0.3	0.2	6	*D*	0.7	—	—	2.8	—	—	—	2.5	2.8	2.7	3.0
*nitens**	—	8	—	0.2	—	—	—	—	2.2	—	—	—	—	—	—	—	—
victoria†	5:1:5	7	0.5	0.2	6	*D*	0.7	*T*	1.9	2.4	1.4	1.3	0.6	1.8	1.8	2.0	2.0
coracina																	
cancellata‡	2:1:2	6-8	0.3	0.2	8	*D*	0.8	*C/C*	2.4	2.2	1.3	1.2	0.6	2.5	2.6	2.8	3.0
coracina‖	2:1:2	7	0.3	0.2	8	—	—	*T*	1.5	2.2	2.0	1.5	—	2.1	2.1	2.1	2.1
enigma‡	5:2:5	7-8	0.4	0.2	8	*D*	0.7	*C/C*	2.7	1.9	1.5	0.9	0.5	2.6	2.7	2.5	2.8
lativittata‡	3:1:3	6-8	0.3	0.2	8	*D*	0.7	*T*	2.9	2.0	1.4	0.9	0.6	2.5	2.7	2.8	2.9
opaca‡	2:1:2	6-7	0.4	0.2	8	*D*	0.7	*T*	3.3	2.0	1.3	0.9	0.6	2.5	2.9	2.6	2.8
maculosa‡	2:1:2	6-7	0.4	0.3	8	*D*	0.8	*C/C*	2.6	2.0	1.0	1.0	0.6	2.2	2.3	2.7	3.0
mirim																	
*baeomyia**	3:1:3	8	—	0.1	8	*C*	—	*T*	1.6	2.2	2.0	—	0.6	1.5	1.7	1.7	2.0
mirim§	2:1:2	8-9	—	0.1	8	*C*	0.7	*T*	1.3	2.3	2.2	—	0.8	1.8	1.8	2.1	2.1
levis‡	3:1:3	8	0.4	0.1	6	*C*	0.7	*T*	1.5	2.3	2.6	1.5	0.7	1.5	1.7	2.0	2.1

* Constructed from the data of Wheeler (1949). † Sturtevant (1942). ‡ The author. § Dobzhansky and Pavan (1943). ‖ Kikkawa and Peng (1938).

♀. Ovipositor plate with about 20 bristles (Fig. 3*D*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, apposed, common trunk 0.3 total length; anterior twice length of posterior.

Internal Genitalia.—♂. Testes orange (10F12), not coiled.

♀. Ventral receptacle very small. Spermatheca spheroidal, heavily chitinized.

Egg Filaments.—7-10, pointed.

Larvae.—Skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 6-7 branches. No anterior spiracle stalks. Posterior spiracles divergent. Site of pupation mainly on stopper.

Relationships.—Tables 1-3.

Distribution.—Moggill (Table 8 and Fig. 1).

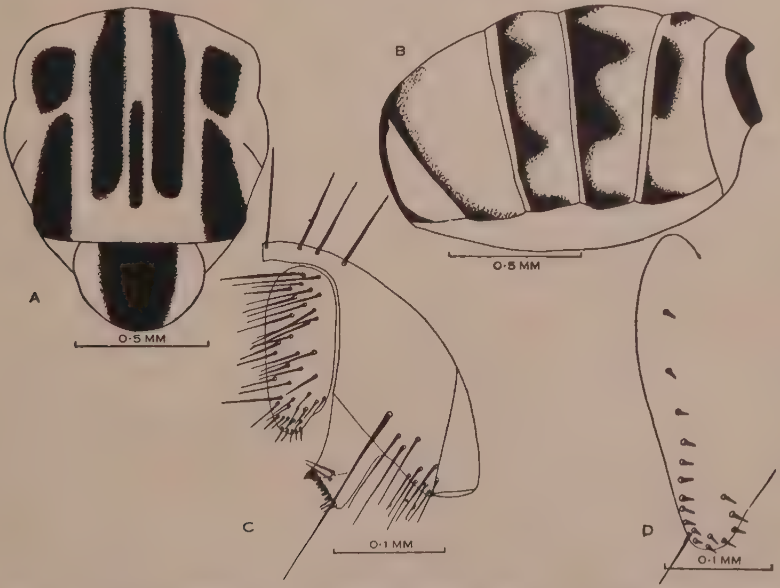

Fig. 4 *A-D.*—*D. enigma*: *A*, ♂ thorax, dorsal view; *B*, ♂ abdomen, dorso-lateral view; *C*, hypopygium; *D*, ovipositor plate.

DROSOPHILA ENIGMA Malloch

Fig. 4*A-D*

Drosophila enigma Malloch, 1927, Proc. Linn. Soc. N.S.W. 50: 6.

General: Brown thorax with white streaks between the 2 submedian rows of acrostichals (Fig. 4*A*).

TABLE 2

SUBGENUS PHOLADORIS: INTERNALS, LIFE HISTORY, AND DISTRIBUTION

Malpighian tubules: *F*, free; *A*, apposed; *Fu*, fused; chitinization: *P*, present; *H*, heavy; relationship pupal post. spir.: *A*, apposed; *D*, divergent; pupation pattern: *N*, not on stopper; *S*, on stopper; larval colour: *L*, lavender; *W*, white, hooklet colour: *Y*, yellow; *B*, blackish

Species Group and Spp.	Malpighian Tubules Ant. — Post.	Testes Colour	Testes Coiling	Spermatheca Chitinization	Ventral Receptacle	Egg Filament Number	Egg Filament Shape	No. of Branches on Pupal Ant. Spir.	Rel. of Pupal Post. Spir.	Pupation Pattern	Larval Colour	Larval Hooklet Colour	Larval Salivary Glands	Distribution**
victoria														
*lebanonensis**	2*F* 0.1 > 2*A* 0.1	Dull yellow	None	*P*	Short	6-10	Curly ends	6-10	*A*	*S*	*W*	*Y*	Unequal	Palae.
*nitens**	—	—	—	—	—	4-8	—	—	—	—	*W*	*Y*	—	Palae.
victoria†	2*F* 0.1 > 2*A* 0.1	"Dark"	None	*P*	Short	4-8	Pointed	4	—	—	*W*	*Y*	Unequal	Near.
coracina														
cancellata‡	0.5 (2*F* 0.1) = 2*A* 0.3	Orange	None	*PH*	Short	7-10	Pointed	6-7	*D*	*S*	*W*	*Y*	Equal	Aust.
coracina‖	—	—	None	—	—	8	—	—	*A*	—	*W*	*Y*	—	Palae. & Ori.
enigma‡	2*F* 0.1 = 2*A* 0.1	Yellow	None	*PH*	Short	5-8	Pointed	5-7	*A*	*S*	*W*	*Y*	Equal	Aust.
lativittata‡	0.5 (2*F* 0.1) = 2*A* 0.2	Orange	None	*PH*	Short	4-6	Pointed	7-8	*D*	*S*	*W*	*Y*	Equal	Aust.
opaca‡	2*F* 0.1 = 2*A* 0.1	Orange	None	*PH*	Short	4-6	Pointed	6-9	*D*	*S*	*W*	*Y*	Equal	Aust.
maculosa‡	0.5 (2*F* 0.1) = 2*A* 0.2	White	None	*PH*	Short	3	Split	8-10	*A*	*S*	*W*	*Y*	Equal	Aust.
mirim														
*baeomyia**	2*F* 0.3 > 2*A* 0.5	Pale yellow	None	*P*	Short	2-8	—	4	*A*	*N*	*L*	*B*	Equal	Near.
mirim§	2*F* 0.5 > 2*A* 0.5	Amber yellow	None	—	Short	6	Pointed	5	—	—	—	—	—	Neotr.
levis‡	2*F* 0.5 = 2*Fu* 0.5	Pale yellow	1*I*, 1*O*	*PH*	4 Coils	4-7	Pointed	6-7	*A*	*N*	*L*	*Y*	Equal	Aust.

* Constructed from the data of Wheeler (1949). † Sturtevant (1942). ‡ The author. § Dobzhansky and Pavan (1943). ‖ Kikkawa and Peng (1938). ** Patterson and Wheeler (1949).

Description

Culture Source.—Moggill, 28.v.1953 (Fig. 1).

Body Length.—♂ 2.5 mm, ♀ 2.8 mm.

Head ♂ and ♀.—Arista with 7-8 branches. Orbital bristles in the ratio of about 5 : 2 : 5. Second oral bristle about 0.4 of 1st. Greatest width of cheeks 0.2 greatest diameter of eyes. Eye colour red (6L8). Carina flat.

Thorax ♂ and ♀.—Brown with a white streak between the 2 submedian rows of acrostichals (Fig. 4*A*). Acrostichal hairs in 8 rows. Prescutellars present. Anterior scutellars divergent. Sterno-index 0.7. Apical bristles on 1st and 2nd tibia; preapicals on all 3. No sex combs.

TABLE 3*

RANGE OF NUMBER OF EGG FILAMENTS OF SPECIES OF PHOLADORIS, RECORDED AS PERCENTAGE OF TOTAL LAID BY FEMALES IN MASS CULTURES

Percentages for Australian species calculated from 50 eggs

Species Group, Spp., and Strain	2	3	4	5	6	7	8	9	10
victoria									
lebanonensis					5	44	44	5	1
nitens			2	37	41	16	3		
victoria 1				32	58	10			
victoria 2				16	55	26	3		
victoria 3			4	7	57	35			
victoria 4			5	22	56	15	2		
victoria 5				12	34	47	7		
victoria 6			6	30	43	21			
victoria 7			4	36	44	16			
victoria 8				25	42	28	5		
victoria 9			1	25	52	21	1		
coracina									
cancellata†						10	32	48	10
enigma†				16	48	32	4		
lativittata†			22	70	18				
opaca†			10	60	30				
maculosa†		100							
mirim									
baeomyia 1	1	2	10	25	42	17	3		
baeomyia 2			13	47	37	3			
baeomyia 3			2	26	59	12	1		
baeomyia 4		1	15	62	19	3			
levis†			10	34	38	18			

* Constructed from the data of Wheeler (1949). † The author.

Wings ♂ and ♀.—Clouding over crossveins. Costal index 2.7, 4th vein index 1.9, 5x index 1.5, 4c index 0.9. Third costal section with heavy spines on its basal 0.5. Length: ♂ 2.6 mm, ♀ 2.7 mm.

Abdomen ♂.—First segment with a black band anteriorly. Second segment with a black band posteriorly, interrupted dorsally and laterally.

Third and 4th segments with a black band posteriorly indented dorsally, dorsolaterally, and ventrolaterally. Fifth and 6th segments with a black band posteriorly (Fig. 4*B*).

♀. Similar to ♂ but with 5th segment similar to 4th, and 6th and 7th segments similar to 5th.

External Genitalia.—♂. Genital arch broad below, about 4 bristles on upper part, about 11 below, heel squarish, undermargin straight, toe squarish. Anal plate oval, free, about 41 bristles evenly distributed, slight rear angle. Primary clasper free, about 3 marginal bristles posteriorly, about 8 primary teeth in a straight line, about 2 bristles anteriorly. Secondary clasper fused onto under side of primary and with 1 tooth (Fig. 4*C*).

♀. Ovipositor plate with about 18 bristles (Fig. 3*D*).

Malpighian Tubules ♂ and ♀.—Two anterior free, common trunk 0.1 total length; 2 posterior apposed, common trunk 0.1 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes yellow (9H1), not coiled.

♀. Ventral receptacle very small. Spermatheca spheroidal, heavily chitinized.

Egg Filaments.—5-8, pointed.

Larvae.—Skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 5-7 branches. No anterior spiracle stalks. Posterior spiracles apposed. Site of pupation mainly on stopper.

Relationships.—Tables 1-3.

Distribution.—Landsborough, 7-9.vi.1952, W. Mather 9/138 8/94, open eucalypt forest. Samford, 22.vi.1952, W. Mather 1/12 2/9, open eucalypt forest. Toowong, 3.viii.1952, W. Mather 0/1 1/4, garden. Montville, 17-20.viii.1952, P. Watkins 0/52 2/46, open eucalypt forest. Carnarvon Gorge, 27-29.v.1954, T. Woodward 2/67 0/64, open eucalypt forest. Moggill (Table 8 and Fig. 1). Probably does not extend into northern Queensland but recorded by Malloch from New South Wales.

DROSOPHILA LATIVITTATA Malloch

Fig. 5*A-D*

Drosophila lativittata Malloch, 1923, Proc. Linn. Soc. N.S.W. 48: 618.

General: Brown thorax with white streaks between the 2 median rows of acrostichals (Fig. 5*A*).

Description

Culture Source.—Moggill, 25.v.1952 (Fig. 1).

Body Length.—♂ 2.8 mm, ♀ 2.9 mm.

Head ♂ and ♀.—Arista with 6-8 branches. Orbital bristles in the ratio of about 3 : 1 : 3. Second oral bristle about 0.3 of 1st. Greatest width of cheek 0.2 greatest diameter of eyes. Eye colour red (5L7). Carina flat.

Thorax ♂ *and* ♀.—Brown with a white streak between the 2 median rows of acrostichals (Fig. 5*A*). Acrostichal hairs in 8 rows. Prescutellars present. Anterior scutellars divergent. Sterno-index 0.7. Apical bristles on 1st and 2nd tibia, preapicals on all 3. No sex combs.

Wing ♂ *and* ♀.—Clear, costal index 2.9, 4th vein index 2.0, 5x index 1.4, 4c index 0.9. Third costal section with heavy spines on its basal 0.6. Length: ♂ 2.5 mm, ♀ 2.7 mm.

Abdomen ♂.—First segment brown. Second, 3rd, and 4th segments with a black band interrupted dorsally, indented dorsolaterally, and with yellow patches ventrolaterally. Fifth segment with black band, interrupted dorsally and laterally. Sixth segment yellow (Fig. 5*B*).

♀. Similar to ♂ but with 5th segment similar to 4th; 6th similar to 5th; and 7th brown, anteriorly, posteriorly, and dorsally.

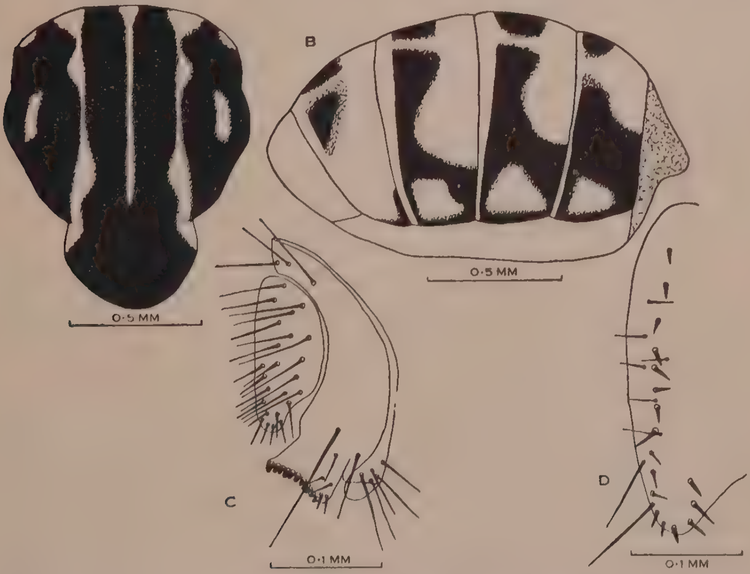

Fig. 5 *A-D*.—*D. lativittata*: *A*, ♂ thorax, dorsal view; *B*, ♂ abdomen, dorsolateral view; *C*, hypopygium; *D*, ovipositor plate.

External Genitalia.—♂. Genital arch broad below, about 3 bristles on upper part, about 8 below, heel squarish, undermargin straight, toe squarish. Anal plate oval, free, about 24 bristles, evenly distributed, slight rear angle. Primary clasper fused to genital arch, no marginal bristles, about 11 primary teeth in concave row, about 4 bristles posteriorly. Secondary clasper absent (Fig. 5*C*).

♀. Ovipositor plate with about 25 bristles (Fig. 5*D*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, apposed, common trunk 0.2 total length; anterior twice length of posterior.

Internal Genitalia.—♂. Testes orange (11A12), not coiled.

♀. Ventral receptacle very small. Spermatheca spheroidal, heavily chitinized.

Egg Filaments.—4-6, pointed.

Larvae.—Skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 7-8 branches. No anterior spiracle stalks. Posterior spiracles divergent. Site of pupation mainly on stopper.

Relationships.—Tables 1-3.

Distribution.—Toowong, 25.v.1952, 1/2 0/0, 5.vi.1952, 2/143 0/58, 3.viii.1952, W. Mather 0/1 1/4, garden. Greenslopes, 4.vi.1952, N. Lavis 1/12 0/2, garden. Landsborough, 7-9.vi.1952, 3/138 4/94, 27-28.ix.1952, W. Mather 6/15 1/12, open eucalypt forest. Condamine River, 11-12.vi.1952, R. Kenny 4/4 6/6, open eucalypt forest. Ipswich, 22-25.viii.1952, 1/31 1/81, 3.viii.1952, J. Davis 1/7 5/50, garden. Maroochydore, 7-8.ii.1953, 1/104 0/90, 8.iii.1953, M. Bleakly 1/74 0/180, open eucalypt forest. Carnarvon Gorge, 27-29.v.1954, T. Woodward 2/67 9/64, open eucalypt forest. Moggill (Table 8 and Fig. 1). Probably does not extend into northern Queensland, but recorded by Malloch from N.S.W. and by A. Clark (personal communication) from Victoria.

DROSOPHILA OPACA, sp. nov.

Fig. 6*A*, *B*

General: Black thorax and abdomen.

Description

Type Culture Source.—Noosa, 9.i.1953 (Fig. 1).

Body Length.—♂ 2.6 mm, ♀ 2.8 mm.

Head ♂ and ♀.—Arista with 6-7 branches. Orbital bristles in the ratio of about 2:1:2. Second oral bristle 0.4 of 1st. Greatest width of cheek 0.2 greatest diameter of eyes. Eye colour red (4L7). Carina flat.

Thorax ♂ and ♀.—Black. Acrostichal hairs in 8 rows. Prescutellars present. Anterior scutellars divergent. Sterno-index 0.7. Apical bristles on 1st and 2nd tibia, preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Transparent. Costal index 3.3, 4th vein index 2.0, 5x index 1.3, 4c index 0.9. Third costal section with heavy spines on its basal 0.6. Length: ♂ 2.5 mm, ♀ 2.9 mm.

Abdomen ♂ and ♀.—All segments black.

External Genitalia.—♂. Genital arch broad below, about 2 bristles on upper posterior margin, about 7 bristles below, heel pointed, under-margin slightly convex, toe absent. Anal plate oval, free, about 30 bristles evenly distributed, rear angle absent. Primary clasper partially fused to genital arch, about 4 marginal bristles posteriorly, about 11 primary teeth in straight row, about 5 scattered bristles posteriorly. Secondary clasper absent (Fig. 6*A*).

♀. Ovipositor plate with about 20 bristles (Fig. 6*B*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, apposed, common trunk 0.1 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes orange (10F12), not coiled.

♀. Ventral receptacle very small. Spermatheca spheroidal, heavily chitinized.

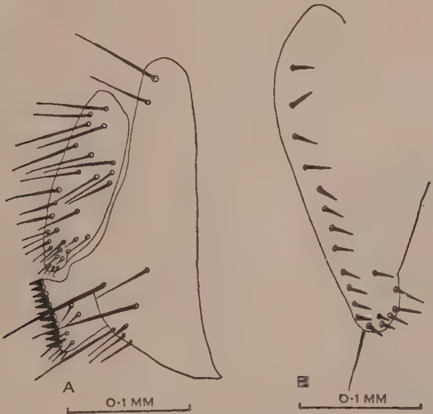

Fig. 6 *A-B.*—*D. opaca*: *A*, hypopygium; *B*, ovipositor plate.

Egg Filaments.—4-6, pointed.

Larvae.—Skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 6-9 branches. No anterior spiracle stalks. Posterior spiracles divergent. Site of pupation mainly on stopper.

Relationships.—Tables 1-3.

Distribution.—Noosa, 9-12.i.1953, W. Dall and E. Grant 0/3 1/11, open eucalypt forest. Clump Point, 3.vi.1953, T. Woodward 1/21 2/8, rain-forest. Moggill (Table 8 and Fig. 1). Collected from both southern and northern Queensland.

Species group MACULOSA, sp. gr. nov.

Black species, anterior scutellar bristles divergent, acrostichal hairs in 8 rows, cheeks 0.3 width of eyes. Male genitalia with squarish heel to genital arch, the latter lightly bristled below; anal plate with not especially dense bristle at lower tip; clasper without numerous fine hairs, and not extended outwards beyond primary teeth which are in a diagonal row across clasper. Posterior malpighian tubules with common trunk 0.2 their total length. Larvae white in colour, ventral hooklets yellow, larval salivary glands of equal size. Egg filaments showing no intraspecific variability and consisting of 3 split filaments.

DROSOPHILA MACULOSA, sp. nov.

Fig. 7*A-D*

General: Thorax with 2 submedian rows of 3 white spots (Fig. 7*A*).

Description

Type Culture Source.—Moggill, 19.xi.1952 (Fig. 1).

Body Length.—♂ 2.7 mm, ♀ 3.0 mm.

Head ♂ and ♀.—Arista with 6-7 branches. Orbital bristles in the ratio of about 2: 1: 2. Second oral bristle about 0.4 of 1st. Greatest width of cheeks 0.3 greatest diameter of eyes. Eye colour red (4L7). Carina flat.

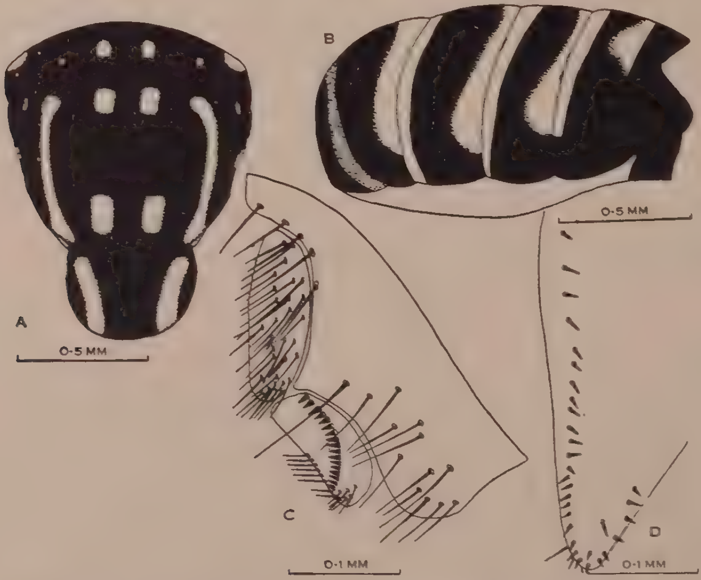

Fig. 7 *A-D.*—*D. maculosa*: *A*, ♂ thorax, dorsal view; *B*, ♂ abdomen, dorsolateral view; *C*, hypopygium; *D*, ovipositor plate.

Thorax ♂ and ♀.—Black with 2 submedian rows of white spots (Fig. 7*A*). Acrostichal hairs in 8 rows. Prescutellars present. Anterior scutellars divergent. Sterno-index 0.8. Apical bristles on 1st and 2nd tibia, preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Clouding over crossveins. Costal index 2.6, 4th vein index 2.0, 5x index 1.0, 4c index 1.0. Third costal section with heavy spines on its basal 0.6. Length: ♂ 2.2 mm, ♀ 2.3 mm.

Abdomen.—♂. First segment black, 2nd to 5th segments with posterior black band which covers entire segment ventrolaterally. Sixth segment with black band posteriorly (Fig. 7*B*).

♀. Similar to ♂ but 6th and 7th segments black.

External Genitalia.—♂. Genital arch broad below, about 5 bristles along upper posterior margin, about 13 bristles below, heel squarish, undermargin slightly concave, toe roundish and below level of heel. Anal plate oval, free, about 30 bristles evenly distributed, rear angle absent. Primary clasper free, about 8 marginal bristles on posterior half, about 17 primary teeth in concave row diagonally across clasper, about 6 bristles posteriorly. Secondary clasper absent (Fig. 7*B*).

♀. Ovipositor plate with about 34 bristles (Fig. 7*C*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, apposed, common trunk 0.2 total length; anterior twice length of posterior.

Internal Genitalia.—♂. Testes white, not coiled.

♀. Ventral receptacle very small. Spermatheca spheroidal, heavily chitinized.

Egg Filaments.—3, split.

Larvae.—Skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 8-10 branches. No anterior spiracle stalks. Posterior spiracles apposed. Site of pupation mainly on stopper.

Relationships.—Tables 1-3.

Distribution.—Moggill (Table 8 and Fig. 1).

Species group LEVIS, sp. gr. nov.

Brown species, anterior scutellar bristles convergent, acrostichal hairs in 6 rows, cheeks 0.1 width of eyes. Male genitalia with squarish heel to genital arch, the latter lightly bristled below; anal plate with not especially dense bristles at lower tip; clasper without numerous fine hairs and not extended outwards beyond primary teeth. Posterior malpighian tubules fused and with common trunk 0.5 their total length. Larvae lavender in colour, ventral hooklets black, larval salivary glands of equal size. Egg filaments showing intraspecific variability between 4 and 7.

DROSOPHILA LEVIS, sp. nov.

Fig. 8*A*-*C*

General: A small brown species.

Description

Type Culture Source.—Maroochydore, 8.iii.1953 (Fig. 1).

Body Length.—♂ 2.0 mm, ♀ 2.1 mm.

Head ♂ and ♀.—Arista with 8 branches. Orbital bristles in the ratio of about 3 : 1 : 3. Second oral bristle about 0.4 of 1st. Greatest width of cheeks 0.1 greatest diameter of eyes. Eye colour red (5L6). Carina flat.

Thorax ♂ and ♀.—Acrostichal hairs in 6 rows. Prescutellars present. Anterior scutellars convergent. Sterno-index 0.7. Apical bristles on 1st and 2nd tibia. Preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Transparent. Costal index 1.5, 4th vein index 2.3, 5x index 2.6, 4c index 1.5. Third costal section with heavy spines on its basal 0.7. Length: ♂ 1.5 mm, ♀ 1.7 mm.

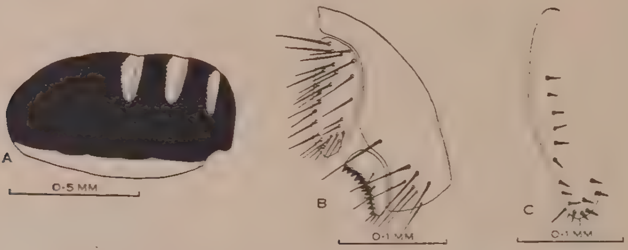

Fig. 8 *A-C.*—*D. levis*: *A,* ♂ abdomen, dorsolateral view; *B,* ♂ hypopygium; *C,* ovipositor plate.

Abdomen.—♂. First segment black. Second to 4th segments with black bands indented with yellow dorsally and laterally. Fifth and 6th segments black (Fig. 8*A*).

♀. Similar to ♂ but with 7th segment also black.

External Genitalia.—♂. Genital arch broad below, about 8 bristles on lower half, heel squarish, undermargin convex, toe squarish and below level of heel. Anal plate oval, free, about 26 bristles, evenly distributed, rear angle absent. Primary clasper free, about 2 marginal bristles posteriorly, about 12 primary teeth in a concave row, and about 2 bristles centrally. Secondary clasper absent (Fig. 8*B*).

♀. Ovipositor plate with about 18 bristles (Fig. 8*C*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.5 total length; 2 posterior, fused, common trunk 0.5 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes pale yellow (10G1) with 1 inner and 1 outer coil.

♀. Ventral receptacle with about 4 coils. Spermatheca spheroidal, heavily chitinized.

Egg Filaments.—4-7, pointed.

Larvae.—Skip, pale lavender, hooklets black, salivary glands equal.

Pupae.—Anterior spiracles with 6-7 branches. No anterior spiracle stalks. Posterior spiracles apposed. Site of pupation mainly not on stopper except for shrivelled larvae.

Relationships.—Tables 1-3.

Distribution.—Noosa, 9-12.i.1953, E. Grant and W. Dall 0/3 1/11, open eucalypt forest. Maroochydore, 7-8.ii.1953, 2/104 4/90, 8.iii.1953, M. Bleakly 12/74 16/180 open eucalypt forest. Clump Point, 3.vi.1953, T. Woodward 3/21 5/8, rain-forest. Moggill (Table 8 and Fig. 1). Collected from southern and northern Queensland.

Subgenus DORSILOPHA Sturtevant

Dorsilopha Sturtevant, 1942, Univ. Tex. Publ. 4213: 28.

DROSOPHILA BUSCKII Coquillett

D. busckii Coquillett, 1901, Ent. News. 12: 18; Patterson, 1943, Univ. Tex. Publ. 4313: 63, Fig. 12, Plate II.

D. rubrostriata Becker, 1908, Mitt. zool. Mus. Berl. 4: 155.

D. plurilineata Villeneuve, 1911, Wien. Ent. Z. 30: 38.

General: Yellow thorax with 3 longitudinal stripes.

Distribution.—Toowong, 6.vii.1952, 1/3 0/26, 10.viii.1952, W. Mather 2/22 5/36, garden. Moggill (Table 5 and Fig. 1). Collected only from southern Queensland but recorded from Western Australia and New South Wales by Malloch and from Victoria by A. Clark (personal communication).

Subgenus SOPHOPHORA Sturtevant

Sophophora Sturtevant, 1939, Proc. Nat. Acad. Sci. Wash. 25: 137.

Species group MELANOGASTER Sturtevant

Melanogaster Sturtevant, 1942, Univ. Tex. Publ. 4213: 28.

Species subgroup MELANOGASTER Hsu

Melanogaster Hsu, 1949, Univ. Tex. Publ. 4920: 121.

DROSOPHILA MELANOGASTER Meigen

D. melanogaster Meigen, 1830, Syst. Beschr. 6: 85; Patterson 1943, Univ. Tex. Publ. 4313: 63, Fig. 14, Plate V.

D. nigriventris Zetterstedt, 1847, Dipt. Scand. 6: 2557 (not Macquart, 1843 Dipt. Exot. 2: 259).

D. ampelophila Loew, 1862, Berl. Ent. Z. 6: 231.

D. uvarum Rondani, 1875, Bull. Com. Agric. Parm.

General: Longitudinal sex comb on distal half of metatarsus of 1st leg and posterior margin of genital arch inconspicuous.

Distribution.—Toowong, 30.v.1952, ?/15 1/18, 5.vi.1952, ?/143 6/58, 21.vi.1952, ?/1 1/3, 6.vii.1952, ?/3 1/16, 13.vii.1952, ?/6 1/22, 8.ii.1952, W. Mather ?/7 4/7, garden. Wooloowin, 29.vi.1952, R. Domorov ?/12

1/29, indoors. Ipswich. 22-25.vii.1952. ? 55 4/57. 3.viii.1952. J. Davis ? 7 2/30, garden. South Johnstone, 23-24.viii.1952. N. Darveniza ? 37 15/32, garden. Tallebudgera Creek, 19.ii.1953, H. Reye ? 8 1/71, open eucalypt forest. Maroochydore, 8.iii.1953, M. Bleakly ? 74 14/180, open eucalypt forest. Tully, 30.iv.1953, L. Webb ? 1 1/4, indoors. Carnarvon Gorge, 27-29.v.1954, T. Woodward ? 67 2/64, rain-forest. Moggill (Table 8 and Fig. 1). Collected from northern and southern Queensland and recorded from New South Wales and South Australia by Malloch, and Victoria by A. Clark (personal communication). Not nearly as prevalent as the closely related *D. simulans*.

DROSOPHILA SIMULANS Sturtevant

D. simulans Sturtevant, 1919, Psyche Camb. Mass. 26: 153; Patterson, 1943, Univ. Tex. Publ. 4313: 63, Fig. 15.

General: Longitudinal sex comb on distal half of metatarsus of 1st leg and posterior margin of genital arch very conspicuous and clam-shaped.

Distribution.—Dunwich, 26.v.1952, P. Watkins and N. Darveniza ? 19 4/35, 19.vii.1952, W. Dall ? 1 2/2, garden. Toowong, 30.v.1952, ? 15 17/18, 5.vi.1952, ? 143 52/58, 21.vi.1952, ? 1 2/3, 13.vii.1952, ? 6 17/22, 27.viii.1952, ? 12 11/16, 3.viii.1952, ? 1 2/4, 10.viii.1952, ? 22 31/36, 8.ii.1953, W. Mather ? 7 3/7, garden. Yeronga, 1.vi.1952, H. Reye ? 6 9/9, garden. Bagara, 2.vi.1952, R. Kenny ? 10 14/15, open eucalypt forest. Urangan, 3.vi.1952, R. Kenny 0 0 1/1, open eucalypt forest. Tolga, 26.v.1952, D. Tranter ? 35 33/33, 28.iv.1953, R. McIntyre ? 78 26/70, garden. Landsborough, 7-9.vi.1952, ? 138 47/94, 27-28.ix.1952, ? 25 5/12, 15.xi.1953, W. Mather ? 18 1/8, open eucalypt forest. Samford, 22.vi.1952, W Mather ? 12 1/9, open eucalypt forest. Ipswich, 22-25.vii.1952, ? 31 73/81, 3.viii.1952, J. Davis ? 7 23/30, garden. South Johnstone, 23-24.viii.1952, N. Darveniza ? 37 36/52, garden. Gin-Gin Creek, 14-16.viii.1952, H. Reye ? 38 24/25, open eucalypt forest. Montville, 17-20.viii.1952, P. Watkins ? 50 30/39, open eucalypt forest. Bulimba, 7.ix.1952, W. Stephenson ? 15 8/5, garden. Somerset Dam, 14.ix.1952, W. Stephenson ? 1 2/2, open eucalypt forest. Coochin Creek, 28.ix.1952, W. Mather ? 1 2/2, open eucalypt forest. Noosa, 9-12.i.1953, W. Dall and E. Grant ? 3 2/11, open eucalypt forest. Maroochydore, 7-8.ii.1953 ? 104 72/90, 8.iii.1953, M. Bleakly ? 74 115/180, open eucalypt forest. Tallebudgera Creek, 19.ii.1953, H. Reye ? 8 4/7, open eucalypt forest. Wooloowin, 10.iii.1953, R. Domorov ? 7 1/9, indoors. Carnarvon Gorge, 27-29.v.1954, T. Woodward ? 67 53/64, rain-forest. Moggill (Table 8 and Fig. 1). Recorded from northern and southern Queensland and from Victoria by A. Clark (personal communication). By far the most ubiquitous species in Queensland.

Species subgroup MONTIUM Hsu

Montium Hsu, 1949, Univ. Tex. Publ. 4920: 121.

Drosophila serrata Malloch

Fig. 9*A-D*

D. serrata Malloch, 1927, Proc. Linn. Soc. N.S.W. 52: Pt. II, 6, Fig. 1.

General: Longitudinal sex comb on 1st and 2nd tarsal segments of 1st leg with about 34 and 18 teeth respectively (Fig. 9*A*).

Description

Culture Source.—Greenslopes, 4.vi.1952 (Fig. 1).

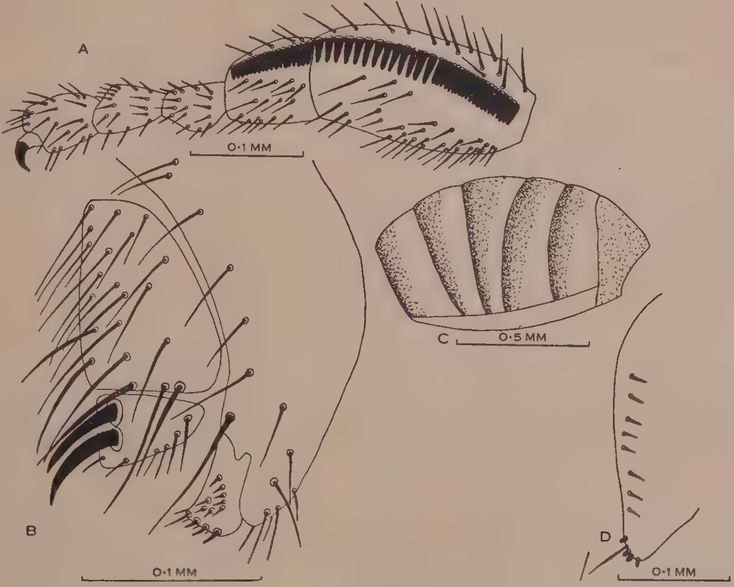

Fig. 9 *A-D.*—*D. serrata*: *A*, tarsus of ♂ fore leg; *B*, hypopygium; *C*, ♂ abdomen, dorsolateral view; *D*, ovipositor plate.

Body Length.—♂ 2.2 mm, ♀ 2.3 mm.

Head ♂ and ♀.—Arista with 8-9 branches. Orbital bristles in the ratio of about 2 : 1 : 2. Second oral bristle about 0.5 of 1st. Greatest width of cheeks 0.2 greatest diameter of eyes. Eye colour red (2L11). Carina ridged.

Thorax ♂ and ♀.—Brown. Acrostichal hairs in 6 rows. Prescutellars absent. Anterior scutellars divergent. Sterno-index 0.6. Apical bristles on 1st and 2nd tibia; preapicals on all 3. Sex comb in the male extending over the 1st and 2nd tarsal segments with about 34 and 18 teeth respectively (Fig. 9*A*).

TABLE 4*

SUBGROUPS MONTIUM AND TAKAHASHII

Carina: *F*, flat; *R*, ridged; wing colour: *T*, transparent; *FC*, faint clouding

Subgroup and Spp.	Orbital Bristles Ratio	Arista Branches	Oral Bristles Ratio	Cheek-Eye Ratio	Carina	Rows of Acrostichals	Sterno-index	Sex Comb Teeth	Wing Colour	Costal Index	4th Vein Index	5x Index	4c Index	Wing Length	Body Length	Distribution†
montium																
auraria	3:1:3	9	1.0	0.2	*F*	6	0.5	26 + 18	*T*	2.0	2.7	2.0	1.5	2.0	2.0	Palae. & Ori.
ficusphila	3:1:3	7	0.8	0.1	*F*	8	0.8	25 + 18	*T*	1.8	2.0	1.5	1.2	2.0	2.2	Palae.
montium	3:1:3	9	1.0	0.1	*F*	6	0.6	25 + 18	*T*	2.1	2.5	2.5	1.5	2.0	2.0	Neotr. Palae., Ori. & Aust.
nipponica	5:1:5	8	0.5	0.3	*F*	6	0.3	15 + 13	*T*	2.0	2.2	1.6	1.1	1.8	1.8	Palae.
rufa	4:1:4	9	0.7	0.1	*F*	6-8	0.6	25 + 18	*T*	2.3	2.5	3.0	1.3	2.1	2.1	Palae.
serrata	2:1:2	8-9	0.5	0.2	*R*	6	0.6	34 + 18	*T*	2.2	2.7	2.5	1.5	1.9	2.2	Aust.
takahashii																
lutea	3:1:3	9	0.7	0.1	*F*	8	0.7		*FC*	2.0	2.2	2.0	1.7	2.1	2.2	Palae.
takahashii‡	2:1:2	8-9	0.5	0.1	*R*	8	0.6		*FC*	2.6	2.1	1.8	1.0	2.0	2.2	Palae., Ori. & Aust.

* Constructed from the data of Kikkawa and Peng (1938). † Patterson and Wheeler (1949). ‡ The author.

Wings ♂ and ♀.—Transparent. Costal index 2.2, 4th vein index 2.7, 5x index 2.5, 4c index 1.5. Third costal section with heavy spines on its basal 0.5. Length ♂ 1.9 mm, ♀ 2.0 mm.

Abdomen.—♂. First segment brown. Second to 6th with posterior brown band (Fig. 9*C*).

♀. Similar to ♂ but with 7th segment black.

External Genitalia.—♂. Genital arch broad above, about 7 bristles along posterior margin, about 8 bristles below, heel absent, undermargin concave, toe rounded. Anal plate triangular, free, about 21 bristles evenly distributed, squarish rear angle. Primary clasper free, about 4 marginal bristles, about 4 primary teeth in a straight line, 2 rows of secondary teeth, about 3 in inner, 4 in outer. Secondary clasper triangular, free, 2 very large bristles on inner margin, about 6 smaller bristles on under margin (Fig. 9*B*).

♀. Ovipositor plate with about 13 bristles (Fig. 9*D*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.2 total length; 2 posterior, free, common trunk 0.1 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes yellow (9J1) with 3 inner and 3 outer coils.

♀. Ventral receptacle with about 7 coils. Spermatheca spheroidal, not chitinized.

Egg Filaments.—2, pointed.

Larvae.—Do not skip, white, hooklets black, salivary glands equal.

Pupae.—Anterior spiracles with 9-11 branches. Posterior spiracles divergent. Ratio (pupal stalk length/pupal body length) = 0.05. Site of pupation not on stopper.

Relationships.—Table 4.

Distribution.—Dunwich, 26.v.1952, P. Watkins and N. Darveniza ?/19 30/35, garden. Bagara 2.vi.1952, R. Kenny ?/10 1/15, open eucalypt forest. Greenslopes, 4.vi.1952, N. Lavis ?/12 2/2, garden. Landsborough, 7-9.vi.1952, ?/138 27/94, 27-28.ix.1952, ?/25 5/12, 15.xi.1953, W. Mather ?/18 7/8, open eucalypt forest. Samford, 22.vi.1952, W. Mather ?/12 1/9, open eucalypt forest. Toowong, 27.vi.1952, W. Mather ?/12 5/16, garden. Gin-Gin Creek, 14-16.viii.1952, H. Reye ?/38 1/25, open eucalypt forest. Montville, 17-20.viii.1952, P. Watkins ?/52 7/46, open eucalypt forest. South Johnstone, 23-24.viii.1952, N. Darveniza ?/23 1/32 Noosa, 9-12.i.1953, W. Dall and E. Grant ?/3 7/11, open eucalypt forest. Maroochydore, 7-8.ii.1953, ?/104 14/90, 8.iii.1953, M. Bleakly ?/24 34/180, open eucalypt forest. Canungra, 8.iii.1953, W. Mather ?/18 12/12, open eucalypt forest. Clump Point, 3.vi.1953, T. Woodward ?/11 1/8, rain-forest. Moggill (Table 8 and Fig. 1). Collected from northern and southern Queensland and also recorded by Malloch from Queensland. After *D. simulans* the most ubiquitous species in Queensland.

Species subgroup TAKAHASHII Hsu

Takahashii Hsu, 1949, Univ. Tex. Publ. 4920: 122.

DROSOPHILA TAKAHASHII Sturtevant

Fig. 10*A*-*D*

D. takahashii Sturtevant, 1927, Phil. J. Sci. 32: 371; Kikkawa and Peng, 1938, Jap. J. Zool. 7: 538, Fig. 19.

General: Sex comb in transverse rows, 6 on metatarsus, distal 2 prominent; 2 on 1st tarsal segment, prominent (Fig. 10*A*).

Description

Culture Source.—Samford 22.vi.1952 (Fig. 1).

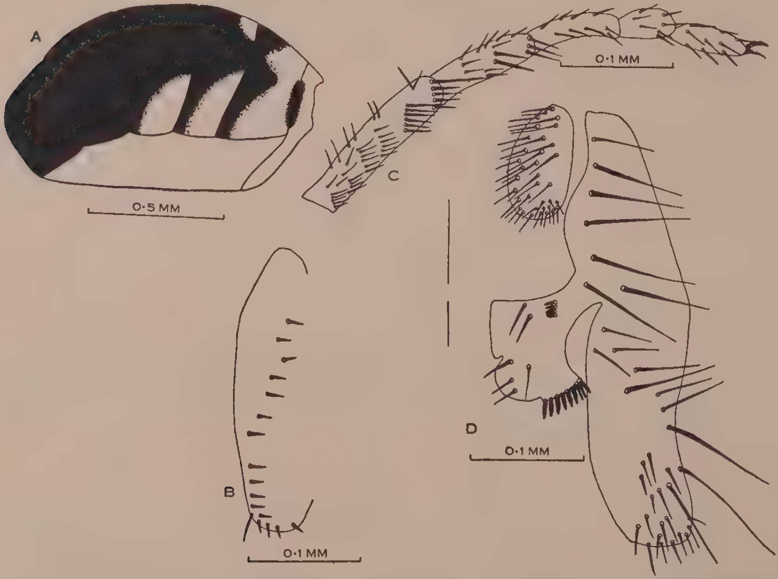

Fig. 10 *A*-*D*.—*D. takahashii*: *A*, ♂ abdomen, dorsolateral view; *B*, ovipositor plate; *C*, tarsus of ♂ fore leg; *D*, hypopygium.

Body Length.—♂ 2.2 mm, ♀ 2.5 mm.

Head ♂ and ♀.—Arista with 8-9 branches. Orbital bristles in the ratio of about 2: 1: 2. Second oral bristle about 0.5 of 1st. Greatest width of cheeks 0.1 greatest diameter of eyes. Eye colour red (2K11). Carina ridged.

Thorax ♂ and ♀.—Brown. Acrostichal hairs in 8 rows. Prescutellars absent. Anterior scutellars convergent. Sterno-index 0.6. Apical bristles on 1st and 2nd tibia, preapicals on all 3. Sex comb in the ♂ in transverse rows, 6 on 1st tarsal segment, distal 2 prominent, 2 on 2nd tarsal segment, prominent (Fig. 10*A*).

Wings ♂ and ♀.—Faintly clouded. Costal index 2.6, 4th vein index 2.1, 5x index 1.8, 4c index 1.0. Third costal section with heavy spines on its basal 0.4. Length: ♂ 2.0 mm, ♀ 2.3 mm.

Abdomen.—♂. First segment yellow. Patch of black laterally on junction of 1st and 2nd segments. Second segment with a black band posteriorly, indented anteriorly, dorsally, and ventrolaterally. Third and 4th segments with black band indented ventrolaterally. Fifth and 6th segments black (Fig. 10*A*).

♀. Similar to ♂ but with 7th segment black.

External Genitalia.—♂. Genital arch of uniform width, about 34 bristles evenly distributed, heel rounded, undermargin convex, toe rounded, and at same level as heel. Anal plate oval, free, about 34 bristles evenly distributed, rear angle absent. Primary clasper attached by stalk to genital arch, no marginal bristles, about 9 primary teeth in straight row on undermargin, about 4 secondary teeth in a row near base of clasper and about 6 scattered bristles. Secondary clasper absent (Fig. 10*D*).

♀. Ovipositor plate with about 17 bristles (Fig. 10*B*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.2 total length; 2 posterior, free common trunk 0.1 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes pale yellow (10G1), with 2 inner and 4 outer coils.

♀. Ventral receptacle with about 10 coils. Spermatheca spheroidal and chitinized.

Egg Filaments.—2, pointed.

Larvae.—Do not skip, white, hooklets black, salivary glands equal.

Pupae.—Anterior spiracles with 4-5 branches. Posterior spiracles divergent. Ratio (pupal stalk length/pupal body length) = 0.06. Site of pupation not on stopper.

Relationships.—Table 4.

Distribution.—Montville, 17-20.viii.1952, P. Watkins ?/51 7/46, open eucalypt forest. Binna Burra, 9-10.xii.1952 ?/35 15/43, 13-14.i.1953, W. Mather ?/40 28/51, rain-forest. Moggill (Table 8 and Fig. 1). Previously recorded by Kikkawa and Peng (1938) from Formosa and China.

Species subgroup ANANASSAE Hsu

Ananassae Hsu, 1949, Univ. Tex. Publ. **4920**: 122.

DROSOPHILA ANANASSAE Doleschall

D. ananassae Doleschall, 1858, Nat. Tijd. **17**: 128, 129; Patterson, 1943, Univ. Tex. Publ. **4313**: Fig. 16, Plate II.

D. imparata Walker, 1859, Proc. Linn. Soc. **3**: 126, 164.

D. similis Lamb, 1914, Trans. Linn. Soc. **3**: 347.

D. caribbea Sturtevant, 1916, Ann. Ent. Soc. Amer. **9**: 335.

D. errans Malloch, 1934, Brit. Mus. (Nat. Hist.) **6**: 301.

General: Transverse sex combs on 1st leg; 2 on 1st tarsal segment and 1 on 2nd tarsal segment.

Distribution.—Tolga, 28.iv.1953, R. McIntyre ?/78 50/70, garden. Tully, 30.iv.1953, L. Webb ?/1 3/4, indoors. Babinda, 4.v.1953, L. Webb ?/13 4/5, rain-forest. Thursday I., 26.vii.1953, D. Tranter ?/7 12/12, garden. Moggill (Table 8 and Fig. 1). Only collected from northern Queensland.

Species group DISPAR, sp. gr. nov.

Dark species, mid-orbital bristle small, 9-10 arista branches, medium size 2nd oral bristle, 8 rows of acrostichals, prescutellars absent, anterior scutellars convergent, sterno-index about 0.5, preapicals of 1st leg of normal length, sex combs absent, no sclerotized areas on 5th abdominal tergite, wings transparent, wing behaviour normal. External male genitalia having anal plate extended into a very prominent finger-like projection. Testes yellow and short, ventral receptacle with about 8 coils. Eggs with 2 filaments expanded apically, larvae do not skip.

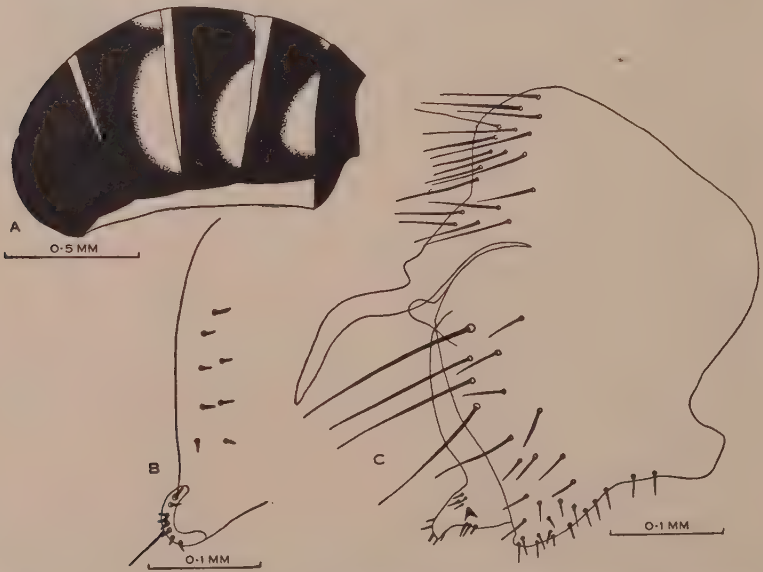

Fig. 11 *A-C*.—*D. dispar*: *A*, ♂ abdomen, dorsolateral view; *B*, ovipositor plate, *C*, hypopygium.

DROSOPHILA DISPAR, sp. nov.

Fig. 11*A-C*

General: Tip of anal plate extended into a very prominent finger-like projection (Fig. 11*C*).

Description

Type Culture Source.—Samford, 22.vi.1953 (Fig. 1).

Body Length.—♂ 2.3 mm, ♀ 2.5 mm.

Head ♂ and ♀.—Arista with 9-10 branches. Orbital bristles in the ratio of about 4 : 1 : 4. Second oral bristle about 0.9 of 1st. Greatest width of cheeks 0.1 greatest diameter of eyes. Eye colour red (3L10). Carina ridged.

Thorax ♂ and ♀.—Brown. Acrostichal hairs in 8 rows. Prescutellars absent. Anterior scutellars convergent. Sterno-index 0.5. Apical bristles on 2nd tibia, preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Transparent. Costal index 2.7, 4th vein index 2.0, 5x index 2.0, 4c index 1.0. Third costal section with heavy spines on the basal 0.6. Length ♂ and ♀ 2.4 mm.

Abdomen.—♂. First segment black. Second, 3rd, and 4th segments with black bands indented dorsally and laterally. Fifth and 6th segments black (Fig. 11*A*).

♀. Similar to ♂ but with 7th segment also black.

External Genitalia.—♂. Genital arch with anterior margin strongly convex, about 31 bristles on lower posterior margin and undermargin, heel prominent, undermargin concave, toe prominent and below level of heel. Anal plate, fused to genital arch and with tip extended into a very prominent finger-like projection, about 18 bristles evenly distributed. Primary clasper fused to genital arch, about 8 marginal bristles, about 1 primary tooth and about 4 bristles. Secondary clasper fused to genital arch and free of bristles (Fig. 11*C*).

♀. Ovipositor plate with about 17 bristles (Fig. 11*B*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, free, common trunk 0.05 total length; anterior and posterior of equal length.

Internal Genitalia.—♂. Testes yellow (9I5) with 3 inner, and 2½ outer coils.

♀. Ventral receptacle with about 8 coils. Spermatheca spheroidal, chitinized.

Egg Filaments.—2, pointed.

Larvae.—Do not skip, white, hooklets black, salivary glands equal.

Pupae.—Anterior spiracles with 9-12 branches. Posterior spiracles divergent. Ratio (pupal stalk length/pupal body length) = 0.05. Site of pupation not on stopper.

Relationships.—Table 5.

Distribution.—Landsborough, 7-9.vi.1952, W. Mather ?/138 2/94, open eucalypt forest. Samford, 22.vi.1952, W. Mather ?/12 2/9, open eucalypt forest. Binna Burra, 19.vii.1952, 0/0 1/1, 9-10.xii.1952, ?/35 28/43, 13-14.i.1953, W. Mather ?/40 23/51, rain-forest. Moggill (Table 8 and Fig. 1).

TABLE 5*

SUBGENUS SOPHOPHORA

Character	*D. dispar*†	Groups						
		saltans	*willistoni*	*melanogaster*	*obscura*	*aligitans*	*nannoptera*	*bromeliae*
Mid-orb. bristle	Small				Large			
Arista branches	9-10							7-9
2nd Oral bristle	Medium				Small			
Rows of acrost.	8					6	8	8
Prescutellars	Absent						Enlar. hairs	Absent
Ant. scutellars	Convergent	Divergent	Divergent	Convergent	Convergent	Divergent	Convergent	
Sterno-index	0.4-0.7	0.3-0.4	0.3	0.5-0.6	0.6			
Preap. 1st leg	Normal				Usu. long			
Sex combs	Absent	Absent	Absent	Present	Present			
5th Abdom. tergite	No sclerotized areas	1 or 2 sclerotized areas	No sclerotized areas	No sclerotized areas	No sclerotized areas			
Wing colour	Transparent					Clouded Crossveins		Clear or light
Wing behaviour	Normal					Constantly waving		
Testes	Yellow and short	Long spiral	Med. long spiral	Med. long spiral			Orange and spiral	
Ventral receptacle	8 Coils	Long fine	Long fine	Rather long			Long and loosely coiled	
Egg filaments‡	2	2	2				2 Long	
Larvae	Do not skip			Do not skip	Do not skip			
Colour	Dark	Dark	Yellowish	Yellowish	Dark	Reddish	Dull black	Dull
Habitat								||
Chief distribution	Queensland	Tropical America	Tropical America	Trop. and Subtrop. Old World	N. Temp. Zone	Mexico	Mexico	Central S. America

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* Constructed from the data of Patterson and Stone (1952). † The author. ‡ Expanded apically. || Usually on flowers.

Subgenus DROSOPHILA Fallén

Drosophila Fallén, 1823, Diptera Sueciae Geomyzides. Part 2: p. 4.

Species group REPLETA Sturtevant

Repleta Sturtevant, 1942, Univ. Tex. Publ. 4213: 5.

Species subgroup HYDEI Wharton

Hydei Wharton, 1944, Univ. Tex. Publ. 4445: 178; Wheeler, 1949, Univ. Tex. Publ. 4920: 182.

DROSOPHILA HYDEI Sturtevant

D. hydei Sturtevant, 1921, Carneg. Instn. Publ. 301: 101; Patterson, 1943, Univ. Tex. Publ. 4313: 126, Fig. 37, Plate VIII.

General: Thorax with bristles arising from black spots but no lateral abdominal yellow spots.

Distribution.—Tallegudgera Creek, 16.ii.1953, H. Reye 5/8 1/7, open eucalypt forest. Maroochydore, 8.iii.1953, M. Bleakly 0/74 1/180, open eucalypt forest. Moggill (Table 8 and Fig. 1). Only collected from southern Queensland and from Victoria by A. Clark (personal communica- it from Victoria, and Malloch from New South Wales and South Australia.

Species subgroup REPLETA Wharton

D. repleta Wharton, 1944, Univ. Tex. Publ. 4445: 178; Wheeler, 1949, 4920: 182.

DROSOPHILA REPLETA Wollaston

D. repleta Wollaston; 1858, Ann. Mag. Nat. Hist. 41: 117; Patterson, 1943, Univ. Tex. Publ. 4313: 117; Fig. 32, Plate VII.

D. punctulata Loew, 1862, Berlin Ent. Z. 6: 232.

D. adspersa Mik, 1886, Wien Ent. Z. 5: 328.

General: Thorax with bristles arising from black spots, lateral abdominal yellow spots and white testes.

Distribution.—Wooloowin, 29.vi.1952, ?/12 18/20, 10.iii.1953, R. Domorov ?/7 8/9, indoors. Tallebudgera Creek, 16.ii.1953, H. Reye ?/8 1/7, open eucalypt forest. Moggill (Table 8 and Fig. 1). Only collected from southern Queensland, but Malloch has recorded it from New South Wales.

Species subgroup MULLERI Wharton

Mulleri Wharton, 1944, Univ. Tex. Publ. 4445: 178.

DROSOPHILA VERSICOLOR, sp. nov.

Fig. 12*A-C*

General: Thorax with bristles arising from black spots, with lateral abdominal yellow spots (Fig. 12*A*) and orange testes.

Description

Type Culture Source.—Moggill, 23.xi.1952 (Fig. 1).

TABLE 6

SUBGROUP MULLERI: EXTERNALS

S, sulcate; *F*, flat; *C*, convergent; *T*, transparent; *R*, ridged; *D*, divergent; *C/C*, clouding over crossveins

Species	Orbital Bristles Ratio	Arista Branches	Oral Bristles Ratio	Cheek-Eye Ratio	Carina	Rows of Acrostichals	Anterior Scutellars	Sterno-index	Wing Colour	Costal Index	4th Vein Index	5x-Index	4c-Index	3rd Costal Section Ratio	Wing Length ♂ (mm)	Wing Length ♀ (mm)	Body Length ♂ (mm)	Body Length ♀ (mm)
*aldrichi**	2:1:2	7	0.3	0.3	*S*	8	*C*	0.8	*T*	2.6	2.2	1.3	1.1	0.3	2.2	—	2.5	—
anceps†	2:1:2	8	0.4	0.2	*R*	8	*C*	0.7	*C/C*	3.0	1.7	1.2	0.9	0.5	2.9	3.2	3.0	3.2
arizonensis‡	3:2:4	7	0.3	0.3	*S*	8	*C*	0.8	*T*	2.4	1.7	1.4	1.0	0.3	2.0	2.1	2.3	2.6
buzzatii‡	3:1:3	7	0.3	0.3	*S*	8	*C*	0.8	*T*	2.7	1.6	1.1	0.9	0.3	2.0	2.1	2.4	2.6
hamatofila‡	4:1:4	7	0.5	0.3	*S*	8	*C*	0.8	*T*	3.1	1.6	1.3	0.9	0.3	2.3	2.5	2.5	2.9
hexastigma†	3:1:3	7	—	0.2	—	8	*C*	—	*T*	3.6	1.5	1.0	0.7	0.4	3.5	3.5	3.2	3.5
longicornis‡	3:1:3	7	0.5	0.3	*S*	8	*C*	0.8	*C/C*	3.2	1.9	1.3	0.9	0.3	2.2	2.5	2.6	2.9
*mainlandi**	2:1:3	7	0.5	0.3	*S*	8	*C*	0.8	*C/C*	3.4	1.6	1.1	0.8	0.3	2.7	—	2.8	—
meridiana‡		8	—	0.3	*S*	8	*C*	0.8	*C/C*	2.6	1.9	1.7	1.1	0.4	2.2	2.2	2.3	2.3
*mojavensis**	2:1:2	7	0.5	0.3	*S*	8	*C*	0.8	*T*	2.9	1.8	1.3	0.9	0.3	2.0	2.3	2.4	2.6
*mulleri**	2:1:2	7	0.3	0.3	*S*	8	*C*	0.7	*T*	2.8	2.0	1.3	1.0	0.3	2.2	2.4	2.6	2.8
peninsularis‡	3:1:3	8	0.3	0.3	*S*	8	*C*	0.8	*T*	2.5	1.6	1.3	1.0	0.5	2.2	—	2.7	3.4
racemova†	4:1:3	7	0.5	0.4	*F*	8	*C*	0.6	*T*	3.0	1.8	1.3	0.9	0.5	3.2	3.9	3.5	4.7
ritae‡	2:1:2	7	1.0	0.3	*S*	8	*D*	0.8	*T*	2.8	1.5	1.1	1.1	0.3	2.2	2.6	2.5	3.3
*spenceri**	2:1:—	8	0.5	0.3	*S*	8	*C*	0.7	*T*	3.0	1.7	1.4	1.2	0.4	4.0	—	4.2	—
subviridis†	2:1:—	8	1.0	0.3	*S*	8	*C*	0.8	*C/C*	3.8	1.5	1.1	0.9	0.5	2.8	—	3.1	—
versicolor‖	2:1:2	7-8	0.3	0.3	*S*	6	*C*	0.6	*T*	2.9	1.7	1.2	0.9	0.3	2.1	2.3	2.5	2.7

* Constructed from the data of Patterson (1943). † Patterson and Mainland (1944). ‡ Patterson and Wheeler (1942). ‖ The author.

Body Length.—♂ 2.5 mm, ♀ 2.7 mm.

Head ♂ and ♀.—Arista with 7-8 branches. Orbital bristles in the ratio of about 2: 1: 2. Second oral bristle about 0.3 of 1st. Greatest width of cheeks 0.3 greatest diameter of eyes. Eye colour red (2L11). Carina sulcate.

Thorax ♂ and ♀.—Grey with bristles arising from black spots. Acrostichal hairs in 6 rows. Prescutellars absent. Anterior scutellars convergent. Sterno-index 0.6. Apical bristles on 1st and 2nd tibia, preapicals on all 3. No sex combs.

Wings ♂ and ♀.—Transparent. Costal index 2.9, 4th vein index 1.7, 5x index 1.2, 4c index 0.9. Third costal section with heavy spines on its basal 0.3. Length ♂ 2.1 mm, ♀ 2.3 mm.

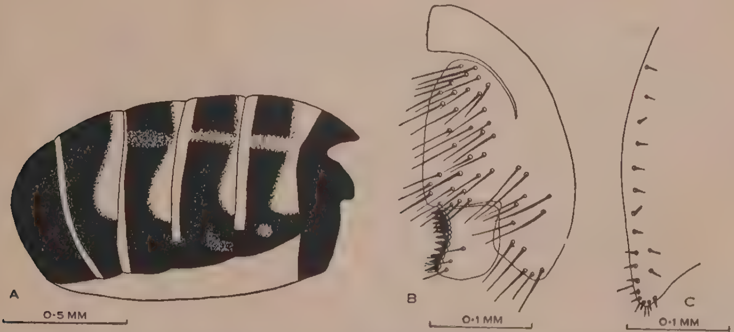

Fig. 12 *A-C.*—*D. versicolor*: *A*, ♂ abdomen, dorsolateral view; *B*, hypopygium; *C*, ovipositor plate.

Abdomen.—♂. First segment black. Second and 3rd segments with a black band posteriorly interrupted dorsally with brown, indented dorsolaterally from the front and with a yellow patch ventrolaterally. Fourth segment similar to 3rd but with no yellow patch. Fifth segment with black band posteriorly indented dorsolaterally from the front. Sixth segment black (Fig. 12*A*).

♀. Similar to ♂ but in addition 7th segment black.

External Genitalia.—♂. Genital arch slightly broader below, about 12 bristles on lower half, heel slightly rounded, undermargin straight, toe rounded and above level of heel. Anal plate oval and fused to genital arch, about 33 bristles evenly distributed. Primary clasper free, about 3 marginal bristles, about 11 primary teeth in a concave row, about 3 bristles posteriorly. Secondary clasper absent (Fig. 12*B*).

♀. Ovipositor plate with about 22 bristles (Fig. 12*C*).

Malpighian Tubules ♂ and ♀.—Two anterior, free, common trunk 0.1 total length; 2 posterior, fused, common trunk 0.1 total length; anterior and posterior of equal length.

TABLE 7

SUBGROUP MULLERI: INTERNALS, LIFE HISTORY, AND DISTRIBUTION

Testes: *I*, inner; *O*, outer; spermatheca: *A*, absent; *P*, present; *L*, light

Species	Testes		Spermatheca Chitinization	Ventral Recept. Coils	Egg Fil. Shape	Branches on Pupal Ant. Spir.	Distribution‖
	Colour	Coiling					
*aldrichi**	Orange	$2I + 2O$	*A*	0	Pointed	9	Near. and Neotr.
anceps†	Yellow	$2I + 2O$	*A*	28	—	12	Near.
arizonensis‡	Orange	$3I + 3O$	*PL*	17	Pointed	11	Near.
buzzatii‡	Orange	$3I + 3O$	*A*	14	Pointed	14	Neotr. & Palae.
hamatofila‡	Yellow	$4I + 5O$	*P*	15	Hooked	11	Near. & Neotr.
hexastigma†	Orange	—	*A*	28	Wavy	18	Near.
longicornis‡	Yellow	$2I + 3O$	*P*	15	Pointed	12	Near. & Neotr.
*mainlandi**	Yellow	$3I + 3O$	*A*	15	—	12	Near.
meridiana‡	Cream	$2I + 3O$	*P*	17	Pointed	19	Near.
*mojavensis**	Yellow	$2\frac{1}{2}I + 2O$	*A*	15	Pointed	11	Near.
*mulleri**	Apricot yellow	$2I + 3O$	*A*	20	Pointed	10	Near. & Neotr.
peninsularis‡	Yellow	$2\frac{1}{2}I + 3O$	*PL*	24	Wavy	15	Near.
racemova†	Yellow	$4I + 4O$	*A*	28	—	10	Near. & Neotr.
ritae‡	Yellow	$2I + 3O$	*A*	18	Pointed	17	Near. & Neotr.
*spenceri**	Yellow	13	*A*	35	—	—	Near.
subviridis†	Yellow	$9I + 9O$	*A*	70	Pointed	—	Near.
versicolor§	Orange	$1I + 2O$	*PL*	12	Pointed	9-14	Aust.

* Constructed from the data of Patterson (1943). † Patterson and Mainland (1944). ‡ Patterson and Wheeler (1942). ‖ Patterson and Wheeler (1949). § The author.

Internal Genitalia.—♂. Testes orange (11F12), 1 inner and 2 outer coils.

♀. Ventral receptacle with about 12 coils. Spermatheca spheroidal and lightly chitinized.

Egg Filaments.—4, pointed.

Larvae.—Do not skip, white, hooklets yellow, salivary glands equal.

Pupae.—Anterior spiracles with 9-14 branches. Posterior spiracles apposed. Ratio (pupal stalk length/pupal body length) = 0.2. Site of pupation not on stopper.

Relationships.—Tables 6 and 7.

Distribution.—McIntyre River, 18-19.ix.1953, E. Grant ?/27 13/13, open eucalypt forest. Moggill (Table 8 and Fig. 1). Only collected from southern Queensland.

Species group IMMIGRANS Sturtevant

Immigrans Sturtevant, 1942, Univ. Tex. Publ. 4213: 32.

DROSOPHILA IMMIGRANS Sturtevant

D. immigrans Sturtevant, 1921, Publ. Carneg. Instn. 301: 101; Patterson, 1943, Univ. Tex. Publ. 4313: 180, Fig. 61, Plate X.

General: A comb-like series of stout bristles on femur of 1st leg, eyes red and 3rd costal section with heavy bristles on its basal quarter.

Distribution.—Dunwich, 26.v.1952, P. Watkins and N. Darveniza 2/19 1/35, garden. Cairns, 4.vi.1952, D. Tranter 4/7 0/0, 24.vi.1953, R. McIntyre 2/4 0/0, garden. Landsborough, 7-9.vi.1952, 6/138 6/94, 27-28.ix.1952, W. Mather 4/75 1/12, open eucalypt forest. Montville, 17-20.viii.1952, P. Watkins 1/52 0/46, open eucalypt forest. Bulimba, 7.ix.1952, W. Stephenson 2/5 0/8, garden. Moggill (Table 8 and Fig. 1). Collected from both northern and southern Queensland, A. Clark (personal communication) has recorded it from Victoria, and Malloch from New South Wales and Western Australia.

DROSOPHILA SPINOFEMORA Patterson & Wheeler

D. spinofemora Patterson & Wheeler, 1942, Univ. Tex. Publ. 4213: 104.

General.—A comb-like series of stout bristles on femur of 1st leg, eyes orange, 3rd costal section with heavy bristles on its basal half.

Distribution.—Babinda, 4.v.1953, L. Webb 5/13 1/5, rain-forest. Clump Point, 3.vi.1953, T. Woodward 2/21 0/8, rain-forest (Table 8 and Fig. 1). Only recorded from northern Queensland but previously recorded from Hawaii by Patterson and Wheeler and northern Queensland by A. Clark (personal communication).

V. DISCUSSION

(*a*) *Descriptive Technique*

In this study certain descriptive techniques have been used which have not hitherto been used in *Drosophila* systematic work, for example, colour description by reference to a standard colour scale, thorax and abdomen illustrated by simple line drawings, species relationships treated by tabulation, slide material deposited with the type material, and the number of specimens of each species taken at each station expressed as a fraction of the total catch.

Further, an attempt has been made to give exact definitions of the measurements made, and to state the number of specimens examined for each character; mean for quantitative characters and the range for meristic characters.

(*b*) *The Subgenus* Pholadoris

The subgenus *Pholadoris* established by Sturtevant (1942) was redefined by Wheeler (1949). The morphology of the Australian species *D. cancellata, D. enigma, D. lativittata, D. maculosa, D. opaca,* and *D. levis* (Tables 1 and 2) allows their classification in this subgenus but it should be noted that *D. maculosa* has 3 split egg filaments and *D. levis* has fused posterior malpighian tubules thus calling for a widening of the definition of the subgenus in respect of these points.

Wheeler divided the subgenus into the *victoria,* and *mirim* species group. He provisionally placed *D. coracina* in the *victoria* group but pointed out that it may belong to a third species group which had, at that time, no other known members. It is now proposed to erect such a third group—the *coracina* group and to include in it *D. coracina* and the Australian species: *D. cancellata, D. enigma, D. lativittata,* and *D. opaca.*

It is considered justified in establishing a fourth species group for the Australian species *D. maculosa* differing from the *coracina* species group in that there are 3 split egg filaments showing no intraspecific variability and the primary teeth on the clasper are in a diagonal row.

Finally, *D. levis* shows closer relationship to the *mirim* group than to the other groups, but the establishment of a new group, *levis* species group for the species is considered justified because the posterior malpighian tubules are fused and there are 6 rows of acrostichals.

Wheeler (1949) pointed out that *D. bryani* Malloch probably belongs to the *victoria* species group. Harrison (1954) has supported this view by a fuller description of the species, but until such time as the life history, and internal structure of the species are examined, due to the fact that the clasper is not extended outward beyond the primary teeth, it seems more likely that the species belongs to the *coracina* group.

Harrison (1954) has assigned *D. samoensis* Harrison tentatively to the *mirim* group but, although the matter cannot be settled until the malpighian tubules are examined, it seems likely that, because there are 6 rows of acrostichals, and the external male genitalia are similar to *levis,* this species should be provisionally placed in the *levis* group.

Harrison (1954) has also assigned *D. marjoryae* to the subgenus, but, until the male external genitalia, certain internal structures, and the life history are studied, it is not possible to assign this species to a species group. Harrison remarks on the wing indices falling outside the range of known members of the subgenus, but, when the Australian species are considered, the wing indices are no longer anomalous.

TABLE 8

GEOGRAPHICAL DISTRIBUTION

From south to north: OEF, open eucalypt forest; RF, rain-forest; G, garden; I, indoors

Station	*D. cancellata*	*D. enigma*	*D. lativittata*	*D. opaca*	*D. maculosa*	*D. levis*	*D. busckii*	*D. melanogaster*	*D. simulans*	*D. serrata*	*D. takahashii*	*D. ananassae*	*D. dispar*	*D. hydei*	*D. repleta*	*D. versicolor*	*D. immigrans*	*D. spinofemora*	Habitat
Southern Queensland																			
McIntyre R.																+			OEF
Binna Burra											+		+						RF
Tallebudgera Ck.								+	+					+	+				OEF
Canungra										+									OEF
Ipswich			+					+	+										G
Dunwich									+	+							+		G
Greenslopes			+							+									G
Yeronga									+										G
Moggill	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+		OEF
Toowong		+	+				+	+	+	+									G
Bulimba									+								+		G
Wooloowin								+	+						+				I
Samford		+							+	+			+						OEF
Coochin Ck.									+										OEF
Landsborough		+	+						+	+			+				+		OEF
Montville		+							+	+	+						+		OEF
Condamine R.			+																OEF
Somerset Dam									+										OEF
Maroochydore			+			+		+	+	+			+						OEF
Noosa				+		+			+	+									OEF
Urangan									+										OEF
Gin Gin Ck.									+	+									OEF
Bagara									+	+									OEF
Carnarvon Gorge		+	+					+	+										OEF
Northern Queensland																			
Tully								+											I
South Johnstone								+	+	+									G
Clump Pt.				+		+				+								+	RF
Babinda												+						+	RF
Tolga												+							G
Cairns																	+		G
Thursday I.												+							G

Likewise, until more is known about the morphology of *D. excepta* Malloch, and *D. anuda* Curran, Wheeler's tentative assigning of these species to the *victoria* group must remain in doubt.

(*c*) *Geographical Distribution*

Despite the fact that southern Queensland has been far more adequately sampled than northern Queensland, it is possible to make certain comparisons between the *Drosophila* fauna of the two regions (Table 8 and Fig. 1). Of the species collected only two: *D. ananassae* and *D. spinofemora* have not been collected in southern Queensland. *D. ananassae* is a cosmopolitan species belonging to the *melanogaster* species group and Sturtevant (1942) has suggested that the distributional records indicate that the group was originally restricted to tropical and subtropical regions of the Old World. The collection of *D. ananassae* from rain-forest at Babinda and rain-forest at Cairns (Dobzhansky 1951, personal communication) may indicate that it forms part of the natural population of northern Queensland.

All species collected in southern Queensland have also been collected at Moggill but this is not surprising as Moggill is a representative area of southern Queensland and very intensive collecting has been done there. But, it should be noted that, on any one day at Moggill, usually only about six species were taken. When intensive collecting is done in northern Queensland, it is considered likely that, many more species will be found.

A particularly interesting feature of the collections from rain-forest at Binna Burra was the presence of only two species: *D. takahashii,* and *D. dispar.* Three collecting trips have been made to Binna Burra in July and December 1953 and January 1954. In July, cold weather prevailed and only one fly, a male *D. dispar* was caught. But, in December and January good collections were made from several different stations, and it was found that only *D. takahashii* and *D. dispar* were present, and in approximately equal numbers, as established from the males. The reasons why there should be only two species in an environment with, presumably, many kinds of ecological niches remain unexplained.

In southern Queensland, the cosmopolitan species *D. simulans* is dominant, and, the Australian species *D. serrata* is subdominant. *D. melanogaster,* which is closely related to *D. simulans,* is not prevalent.

Finally, as has been pointed out previously (Mather 1953), the most interesting feature of the Queensland *Drosophila* fauna is the prevalence of species assignable to the subgenus *Pholadoris,* and Harrison (1954) has also pointed out this feature of the Samoan and Fijian faunas. Thus, additional evidence is to hand, supporting Harrison's suggestion that "in the South Pacific a sizeable proportion of the Drosophila fauna has developed from the *Pholadoris* division of the genus".

VI. ACKNOWLEDGMENTS

Grateful acknowledgment is extended to Professor T. Dobzhansky, Zoology Department, Columbia University, New York, who suggested that this study be undertaken; Professor W. Stephenson, Zoology Department, University of Queensland, for much helpful advice and criticism; Dr. A. B. Walkom, Director of the Australian Museum, Sydney, for permission to examine certain of Malloch's type specimens; Mr. D. J. Lee of the School of Public Health and Tropical Medicine, University of Sydney, for permission to examine others of Malloch's types; Mr. M. Page, and Miss Elaine Hassall for technical assistance; and to the staff and students of the Zoology Department, University of Queensland, for assistance in the collections.

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THE CLASSIFICATION AND DISTRIBUTION OF TABANIDAE (DIPTERA)

III. SUBFAMILIES SCEPSIDINAE AND CHRYSOPINAE

By I. M. MACKERRAS*

(*Manuscript received June 8, 1955*)

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Summary

The following genera are recognized in the subfamilies reviewed in the present paper:

SCEPSIDINAE

Neotropical: *Scepsis* Walk.
Ethiopian: *Adersia* Aust.; *Braunsiomyia* Beq.
Lesneus Surc. is excluded from the Tabanidae.

CHRYSOPINAE

BOUVIEROMYIINI

Nearctic: *Merycomyia* Hine.
Neotropical: *Merycomyia* (northern); *Mesomyia* Macq., subgenus *Veprius* Rond. (southern).
Ethiopian: *Mesomyia* Macq., subgenera *Mesomyia, Perisilvius* End., and *Bacloceras* Aust.; *Dasycompsa* End.; *Pronopes* Loew; *Rhigioglossa* Wied.; *Aegophagamyia* Aust.; *Bouvieromyia* Strand; ?*Triclida* End.
Oriental: *Eucompsa* End.
Australasian: *Mesomyia* Macq., subgenera *Vepriella*, nov. (type *frontalis* Ric.), *Pareucompsa* End., *Lilaea* Walk., *Pseudotabanus* Ric., and *Mesomyia; Phibalomyia* Tayl.; *Pseudopangonia* Ric.

CHRYSOPINI

Palaearctic: *Chrysops* Mg.; *Silvius* Mg., subgenus *Silvius.*
Nearctic: *Chrysops; Silvius,* subgenera *Silvius, Zeuximyia* Philip, and *Assipala* Philip.
Neotropical: *Chrysops; Silvius,* subgenus *Assipala* (northern).

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Ethiopian: *Chrysops.*
Oriental: *Chrysops; Silvius,* subgenus *Silvius* (extreme northern).
Australasian: *Chrysops* (northern).

RHINOMYZINI

Ethiopian: *Tabanocella* Big.; *Sphecodemyia* Aust.; *Orgizomyia* Grünb.; *Thaumastocera* Grünb.; *Thriambeutes* Grünb.; *Hinea* Adams.
Oriental: *Gastroxides* Saund.; *Rhinomyza* Wied.

Surcoufia Kröb. (Palaearctic) and *Melissomorpha* Ric. (northern Oriental) are accepted as presumably Chrysopinae, but cannot be allotted to a tribe from the descriptions. Evaluation of possible subgenera of *Chrysops* is not attempted in the present work.

Subfamily **SCEPSIDINAE** (Bequaert, 1930)

Ninth tergite divided in both sexes of *Adersia*; a single, large, triangular, arched plate in ♀ of *Scepsis.* Eyes bare; ocelli well developed. Frons of ♀ wide (index less than 1), converging or diverging, with or without a callus. Antennae short, pangoniine-like; 3rd segment more or less subulate, 7- or 8-annulate. Palpi very short; 2nd segment bulbous, with an apical pit in both sexes. Proboscis extremely short and weak, but with recognizable labella. Hind tibiae with paired apical spurs. Vein *sc* bare above and below. ♂ and ♀ genitalia of *Adersia* indistinguishable from those of Chrysopinae; ♀ genitalia of *Scepsis* (Fig. 1) quite distinctive. Small to medium sized, pale, sand-dwelling flies.

When the group was provisionally raised to subfamily rank in Part I of this series (Mackerras 1954), only the female of *Scepsis* and the male of *Adersia* had been examined. The additional material now received shows it to have stronger affinities with Chrysopinae than had at first been apparent, and it may well be that it would be best placed as a tribe within that subfamily. The characters of the antennae, palpi, and proboscis, however, set it sharply apart, and it may be allowed to retain its present rank until the included species have been more completely studied. Surcouf's (1921, Pl. 5, Fig. 10a) figure suggests that the females of *Braunsiomyia* may have cerci similar to those of *Scepsis.* Whatever its final taxonomic position, the group will remain of exceptional interest, because it evidently arose at about the time that the primitive tabanid complex was splitting into its two major subdivisions.

Bequaert (1930) noted that Dr. Brauns found *Adersia* and *Braunsiomyia* resting on decayed seaweeds accumulated in the drift on the ocean beach near Port Elizabeth, South Africa, and the specimen of *Scepsis* I have seen was collected on a sea beach. Austen (1912) quoted Dr. Aders as writing that *A. oestroides* was found generally on a hot, sandy bank, where cattle were buried; the carcasses seemed to have a great attraction for these flies. Nothing further seems to be known of the habits or life histories of this group.

Lesneus Surcouf, 1921 (monotypic for *canescens* Surcouf, 1921, French Somaliland) was described as having spurs on all tibiae, and

Mr. Oldroyd has informed me that the type is a therevid. This leaves only three monotypic genera in the subfamily.

Neotropical

Genus SCEPSIS Walker, 1850

Genotype: monotypic for *Scepsis nivalis* Walker, 1850, Brazil.

Species examined.—*nivalis* Walk., ♀, det. Philip.

This appears to be the most primitive member of the group. The 3rd antennal segment is subulate and 8-annulate; frons of ♀ without a callus; eyes of ♂ separated; posterior orbits in both sexes narrow; cells R_5 and M_3 open, vein R_4 angulate or with an appendix.

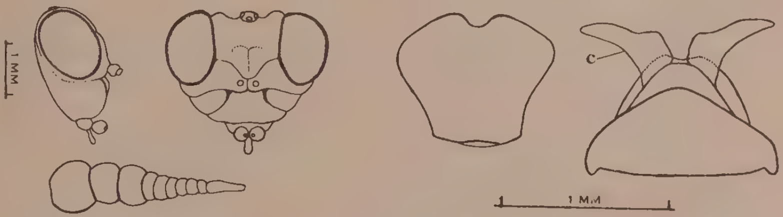

Fig. 1.—*Scepsis nivalis* Walk., female; *c*, cercus. Antenna from a drawing by Mr. Oldroyd.

Female

The ♀ before me shows the following additional characters. Eyes small. Frons converging, wider than long, smoothly tomentose, and covered with evenly arranged short hairs, except for a median triangular area on the lower part. Subcallus not projecting, but clearly marked off from frons, tomentose, with a few hairs on each side above and lateral to antennae. Parafacials wide and long; face only moderately projecting. Palpi with both segments bulbous, about equal in length, and the 2nd with a small, rounded, apical pit. Proboscis little longer than the 2nd palpal segment, but labella recognizable. Thorax with suture and humeral and notopleural lobes unusually well defined. Hind tibial spurs moderately long and slender. Wings with cell Cu_2 narrowly open at margin; vein R_4 with strong appendix. Hypopygium of extraordinary form: 8th sternite rather chrysopine in appearance, and with a shallow notch between the gonopophyses; 9th tergite a broad, triangular, arched, heavily chitinized plate; 10th tergite undivided, forming a rounded lobe just beyond the 9th; cerci (Fig. 1, *c*) narrow, laterally directed, shaped like the head of a bird, and more chitinized than usual.

Distribution.—Brazil (Rio de Janiero).

Ethiopian

Genus ADERSIA Austen, 1912

Genotype: monotypic for *Silvius oestroides* Karsch, 1888, Tanganyika.

Species examined.—oestroides (Karsch), ♂, det. Philip, ♀, det. I.M.M.

I have recently had the good fortune to examine three pairs of this species in excellent condition, kindly sent to me by Dr. E. McC. Callan, of Rhodes University, South Africa.

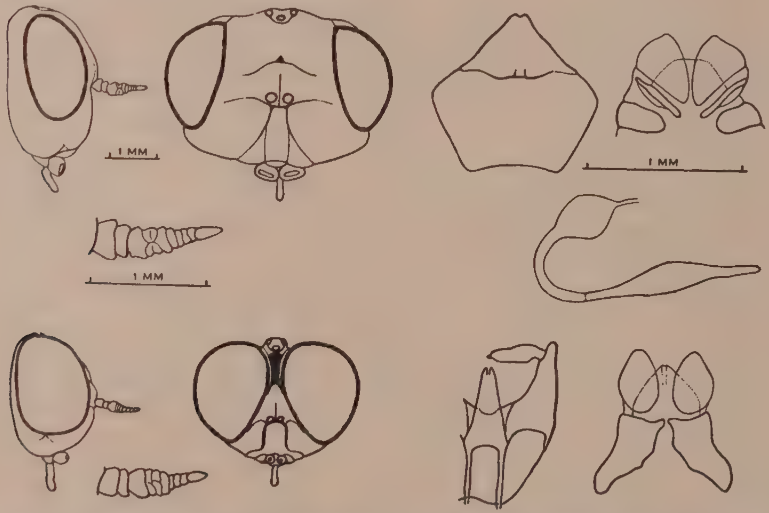

Fig. 2.—*Adersia oestroides* (Karsch). Top series: female, drawn from a specimen 16 mm long; at right, spermatheca, showing swelling on duct. Bottom series: male.

Grey to cream coloured flies, with whitish wings, and green to brown eyes without bands or spots. Distinguished from *Scepsis* by: 3rd antennal segment shorter and wider; frons of ♀ diverging, and eyes rounded above antennae (angulate in *Scepsis*); parafacials shorter; posterior orbits wide; vein R_4 gently curved, without appendix; ♀ genitalia of entirely different structure.

Female

Frons bulging, tomentose, with a minute black callus near lower end; indistinctly marked off from the flat ocellar tubercle above and the tomentose, hairless subcallus below. Parafacials wide and bulging; face rather narrow. Third antennal segment 8-annulate; it appears as if soft, and the basal annuli, though separated by deep furrows, are irregular and rather ill defined. First segment of palpi not swollen; apical pit of second deep, more or less transverse, much larger than in *Scepsis*. Hind tibial spurs slender. Wing with cell Cu_2 closed. Hypopygium (Fig. 2), in striking contrast to *Scepsis*, of completely normal chrysopine form, except that the gonopophyses are more or less completely fused, and form a projecting triangle posteriorly; spermathecal ducts short, with a transparent globular expansion near the elongate spermathecae; their caudal ends larger and paler than in *Scepsis*, and tapering posteriorly.

Male

Smaller and darker than ♀. Eyes rounded, distinctly separated; upper facets not enlarged. Frons narrow, darkened, and with a small, elongate, black callus. Ocellar tubercle very large, filling a deep cleft between the eyes posteriorly. Parafacials bulging forward; face rather sunken. Second segment of palpi not as swollen as in ♀, and proboscis even smaller. Hypopygium with style pointed; aedeagus small, smooth; flagella small.

Distribution.—East and South Africa, from Somaliland to Cape Colony (Bequaert 1930).

Genus BRAUNSIOMYIA Bequaert, 1924

Nom. nov. for *Brodenia* Surcouf, 1921, nec Gedoelst, 1913.

Genotype: monotypic for *Brodenia cinerea* Surcouf, 1921, South Africa.

Separated from *Adersia* by the presence of a broad frontal callus in the ♀; contiguous eyes in ♂; and 7-annulate 3rd antennal segment in both sexes. Bequaert (1930) noted that veins M_2 and M_3 of the wing tend to fade out beyond the discal cell in both *Adersia* and *Braunsiomyia*.*

Distribution.—Cape of Good Hope.

Subfamily **CHRYSOPINAE** Lutz, 1905

Ninth tergite nearly always divided; a pair of large, characteristically shaped plates in ♂ (rarely narrowly united in mid-line); small, widely separated, triangular plates in ♀. Ocelli well developed. Frons usually with well-developed, shining callus. Antennae short or long; 3rd segment with the basal 4 annuli more or less widened and fused, and with a style of 4 or fewer annuli, the usual appearance being of a 5-annulate segment. Proboscis rarely longer than head height; labella well developed, usually with a lateral chitinized bar or zone. Hind tibiae with paired apical spurs, sometimes minute (absent in *Thaumastocera*). Vein *sc* bare or setulose; R_4 rarely with appendix. Style of ♂ simple, more or less bluntly pointed in dorsal view. Caudal ends of spermathecal ducts of ♀ without mushroom-like expansions.

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* These notes are not entirely correct; see Addendum, p. 631.

The great majority of Chrysopinae may be recognized by their well-developed ocelli and hind tibial spurs, 5-annulate 3rd antennal segment, and general resemblance to Tabaninae rather than Pangoniinae. The setulae on *sc* have a limited field of usefulness in separating those that possess them from aberrant Pangoniinae and the remainder from Tabaninae, and it is sometimes useful also that a well-developed appendix to R_4 is uncommon in Chrysopinae. In a few anomalous cases, however, the genitalia provide the only crucial evidence. Most members of this subfamily are blood-suckers.

Division of the subfamily into tribes has presented considerable difficulty. Most authors (Lutz 1909; Enderlein 1922, 1925; Bequaert 1930; Kröber 1932, 1939) have separated *Chrysops* at least tribally from the remainder of the group, including *Silvius,* whereas Philip (1941*a*, 1941*b*) could not recognize this distinction in the Nearctic fauna, but separated off *Merycomyia* from the others. The truth seems to be that the distinction between *Chrysops* and other genera is a good one in regions where *Silvius* does not occur, but not where it does, and that *Silvius* is more nearly related to *Chrysops* than to the rest of the subfamily. Philip, in effect, recognized this when he created the Merycomyiini.

The genitalia have given little assistance in resolving this problem. There are a few unusual forms, such as the much broadened style of the male in *Phibalomyia,* but the only strong indication of a group character is in the laterally compressed "ovipositor" of several Rhinomyzini, and this is not a feature of all the genera which seem in other respects to be closely related.

It is necessary, then, to rely almost entirely on external characters. Looked at broadly, these seem to me to divide the subfamily into three major groups of genera. One represents the ancestral stock, which has probably changed but little since the Mesozoic. The second and third are specialized radiations from that stock, one predominantly Holarctic and the other in tropical Africa. They are not as sharply segregated from one another as could be desired, and there are a few genera which are difficult to place; but they are at least as well defined as corresponding groups which have been given tribal rank in the Tabaninae. It therefore seems logical and convenient to recognize them as tribes, which may be distinguished by the following key.

KEY TO TRIBES OF CHRYSOPINAE

1. Bizarre forms, with modified, sometimes biramous antennae, and nearly always some of the following: flat, shining frons, bulging subcallus, inflated palpi, strongly pictured wings, laterally compressed ♀ terminalia. Vein *sc* setulose, at least below. Ethiopian and Oriental .... Rhinomyzini

Normal to slender forms, with more normal heads; antennae short or long, but never biramous; palpi rarely inflated 2

2. Usually slender species; antennae longer than antero-posterior thickness of head, usually much longer; eyes spotted when alive or relaxed; vein *sc* bare. Predominantly Holarctic, but *Chrysops* cosmopolitan .... Chrysopini

Usually diachlorine- or *Tabanus*-like species; antennae shorter than antero-posterior thickness of head; eyes concolorous or banded when alive or relaxed; vein *sc* setulose or bare. Predominantly Neotropical, Ethiopian, Australasian .... Bouvieromyiini

Certain genera, which were allotted to Silviinae by Enderlein (1925) and Kröber (1932) and to Merycomyiini by Stone (1953), have been transferred to other subfamilies, namely:

To Pangoniinae: *Asaphomyia* Stone, 1953; *Chaetopalpus* Philippi, 1865; *Ectenopsis* Macquart, 1838; *Pseudomelpia* Enderlein, 1922; *Histriosilvius* Kröber, 1930 (tentative); *Metaphara* Enderlein, 1922 (syn. of *Philoliche*); *Dasysilvius* Enderlein, 1922 (syn. of *Pangonius*).

To Scepsidinae: *Adersia* Austen, 1912; *Brodenia* Surcouf, 1921; *Scepsis* Walker, 1850.

To Tabaninae: *Hemichrysops* Kröber, 1930 (personal communication from Fairchild, who has examined the type of the genotype).

Zophina Philip, 1954, was based on old material in imperfect condition. Philip (1954) included it in Chrysopini because the eye showed a suggestion of freckling on brief relaxation; but it seems to be more like *Chaetopalpus* in other respects, and has been listed provisionally under Pangoniinae in Part II of this series (Mackerras 1955).

The following genera are accepted as presumably Chrysopinae, but cannot be allotted to a tribe on available information.

Genus SURCOUFIA Kröber, 1922

Genotype: monotypic for *Surcoufia paradoxa* Kröber, 1922 (= *Diachlorus barbatus* Bigot, 1892), North Africa.

Described as having globular 1st and 2nd antennal segments. Dr. Fairchild has sent me the following notes on the ♂: Eyes bare, holoptic, the large facets about two-thirds of eye area, sharply demarcated from small facets; ocelli large and prominent; labella rather small and slender, with sclerotized plates; *sc* bare above and below; spurs on hind tibiae rather short.

Distribution.—Palaearctic: France; Tunis; Morocco.

Genus MELISSOMORPHA Ricardo, 1906

Genotype: monotypic for *Melissomorpha indiana* Ricardo, 1906, Northern India.

This remarkably bee-like fly has been well illustrated by Surcouf (1921, Pl. 3, Figs. 12a, b), and Dr. Fairchild has kindly sent me the following notes on the type female, which he examined when visiting the British Museum: "Frons broad, parallel-sided, dominated by the enormous ocelligerous tubercle with 3 large ocelli which fills upper half of frons. Lower half of frons sunken, with a small raised arrowhead shaped callus. Eyes bare. Antennae slender; segment 1 twice length of segment 2; segment 3 about twice length of 1 + 2; 3rd segment of an indistinct number of fused basal annuli and 4 terminal annuli. Palpi and proboscis folded under thorax, but the former apparently as in *Chrysops*. The proboscis short, hardly as long as palpi, the theca large, inflated, the labella small, the whole of odd structure. Subepaulet bare, no setae on *sc*. Otherwise as described, and a most perfect mimic of *Apis dorsalis*. The habits must be peculiar, as the mouth-parts hardly seem fitted for blood-sucking."

The resemblance to *Dasycompsa* seems to be due to mimicry of similar models, and I suspect that *Melissomorpha* may belong to Chrysopini rather than Bouvieromyiini.

Distribution.—Northern Oriental: Rungaroom, nr. Darjeeling, U.P.

Tribe BOUVIEROMYIINI (Enderlein, 1922) emend.

Eyes bare or hairy, sometimes banded but never spotted in life. Frons usually medium to narrow, index generally greater than 3; callus usually elongate, occasionally rounded or transverse, rarely absent; most species with a wide frons and callus have hairy eyes. Face truncate or rounded, rarely shining. Antennae shorter than antero-posterior thickness of head; 1st segment little longer than wide; basal part of 3rd usually with well-defined dorsal angle or hump, and style sometimes with fewer than 4

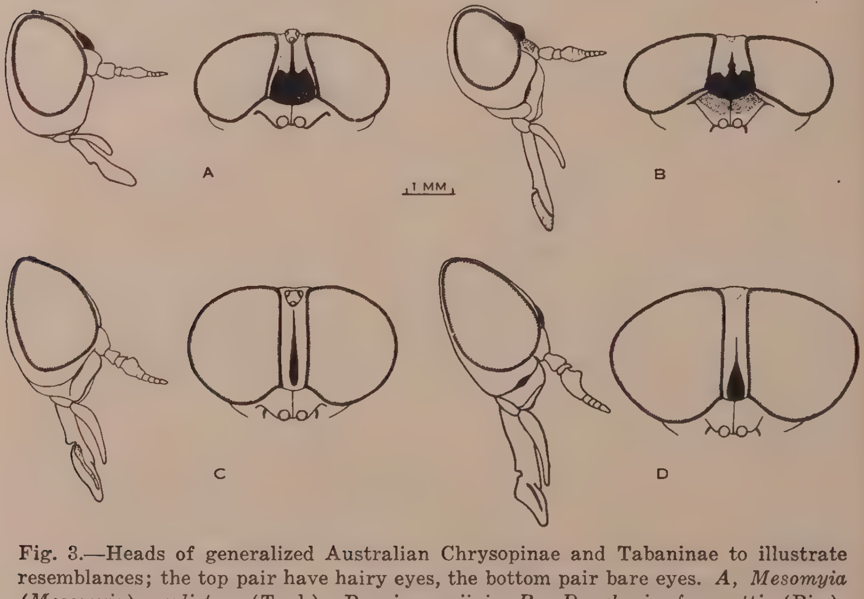

Fig. 3.—Heads of generalized Australian Chrysopinae and Tabaninae to illustrate resemblances; the top pair have hairy eyes, the bottom pair bare eyes. *A*, *Mesomyia* (*Mesomyia*) *cydister* (Tayl.), Bouvieromyiini; *B*, *Dasybasis froggatti* (Ric.), Diachlorini; *C*, *Mesomyia* (*Pseudotabanus*) *distincta* Ric., Bouvieromyiini; *D*, *Cydistomyia postica* (Wied.), Diachlorini.

annuli. Palpi usually slender and tomentose, sometimes relatively wide and soft, never grossly inflated or shining. Wing with vein *sc* setulose or bare; cells R_5 and M_3 occasionally closed, cell Cu_2 closed. Genitalia normal in ♀, occasionally modified in ♂. Mostly small to medium sized, diachlorine-like flies, which are almost confined to the southern hemisphere.

The tribe is a compact one, with little diversity of structure. Its generalized members are only distinguishable from generalized Diachlorini by the essential subfamily characters, and they present precisely similar difficulties in classification at the generic and subgeneric levels. They may therefore be examined as a single complex, before reviewing the genera by zoogeographical regions.

The Mesomyia-Veprius *Complex*

This complex includes the Chilean *Veprius,* the African *Mesomyia* and *Perisilvius,* and the Australian *Lilaea, Pseudotabanus,* and hairy-eyed *"Silvius",* together with some better defined offshoots, which will be considered later. Some of the species have bare eyes, smooth bodies, narrow frons, firm, slender palpi, and a general *Cydistomyia*-like appearance; others have hairy eyes and bodies, wide frons, softer, shorter, more hairy palpi, and a strikingly *Dasybasis*-like appearance (Fig. 3); others are intermediate; and still others are nondescript in appearance. In spite of the superficial diversity, structural differences between the groups are neither substantial nor constant. I believe, therefore, that they should all be treated as belonging to a single, widespread genus, for which *Mesomyia* is the oldest available name,* and which may be defined in the following terms.

Genus MESOMYIA Macquart, 1850

Genotype: originally monotypic for *Mesomyia decora* Macquart, 1850, South Africa.

Generalized, diachlorine-like flies, with eyes of ♂ holoptic, and frons of ♀ tomentose and almost always with a well-developed, sometimes linear, callus. Antennae with 1st and 2nd segments short; basal plate of 3rd occasionally showing traces of annulation, and usually with a blunt or rounded dorsal angle; style with 4, or occasionally 3, annuli. Proboscis short and fleshy, but usually strong; labella large, usually with a lateral chitinous bar. Hind tibial spurs medium to very small. Wing with cells R_5 and M_3 open, Cu_2 closed; vein *sc* setulose or bare, R_4 occasionally with a small appendix. Genitalia of both sexes unmodified, except that the halves of the 9th tergite of the ♂ are sometimes narrowly united in the mid-line, and sometimes incompletely divided into proximal and distal portions.

Distribution.—Neotropical; Ethiopian; Australasian (Fig. 4).

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* Oldroyd and Fairchild have informed me that there is reason to believe that Macquart's "Fourth Supplement" appeared earlier in 1850 than Walker's "Insecta Saundersiana". *Mesomyia,* therefore, has precedence over *Lilaea.*

The question remains, whether any of the groups of species within the genus can be defined with sufficient precision to warrant their recognition as subgenera. There are two major difficulties.

The first is the paucity of structural characters already mentioned. The genitalia in both sexes certainly help to indicate relationships, but the differences observed are not sufficiently precise to be used as primary subgeneric characters. The presence or absence of setulae on the lower side of vein *sc* seemed promising at first, because African species and the Australian *Lilaea* lack them, but it was soon found that they are also absent in one species of *Pseudotabanus* and some of the hairy-eyed Australian species. They may be used, but with reservation. Hairiness of eyes is open to three objections: it grades from imperceptible through perceptible to obvious at the chosen magnification of ×15; perceptibly hairy eyes occur in one or more species of at least three different groups within the genus; and the development of hairs may be subject to environmental influence, as indicated below. The character may be used, but again with the reservation that it requires support from other, independent characters. On the other hand, banding of the eyes (as distinct from the "freckling" of Chrysopini) appears to be limited in this subfamily to three relatively well-defined groups of *Mesomyia*. It is easy to see in fresh or relaxed specimens, and I have given it more weight here than would be proper in corresponding groups of Tabaninae.

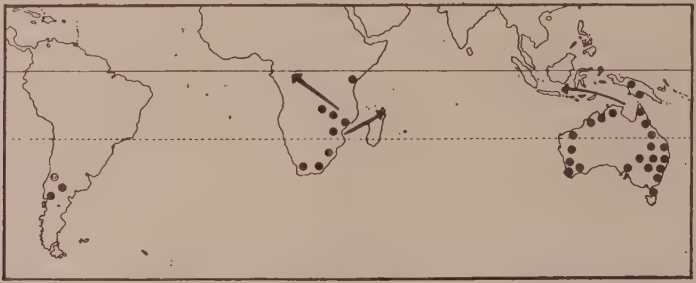

Fig. 4.—Distribution of the genus *Mesomyia*. Arrows indicate outlying distribution of related genera.

Other characters were studied also, but, except for the shape of frons and callus in the female, they proved to be at most of minor supporting value. A further difficulty is presented by the males, which are more uniform than the females and lack their useful frontal characters, without sufficient compensation in distinctive genitalic characters of their own.

It follows from all this that, if subgenera are to be recognized, they will have to be defined, not by single key characters, but by an assemblage of minor characters and trends, which are collectively sufficient to indicate genetic uniformity.

This leads to the second major difficulty, which is that generalized Bouvieromyiini and Diachlorini with bare eyes, narrow frons, and smooth bodies predominate in hotter (sometimes drier) parts of the country, and those with hairy eyes, wide frons, and hairy bodies predominate in cooler districts. The rule is not absolute—one does find bare-eyed species in cooler districts and hairy-eyed ones in warm—but it is sufficiently general in both tribes in Australia and in Diachlorini in South America to demand attention, though it does not appear, on available evidence, to be as clearly indicated in Africa. Banding is more frequent on bare than hairy eyes, and consequently shows the same distributional trend, but I have not been able so far to detect it in other characters.

The phenomenon may be illustrated in Australia by the distribution of the subgenera, particularly the contrast between *Pseudotabanus* and *Mesomyia* (Fig. 12*C*, *D*), by a gradation in hairiness of body and eyes from south to north in the *montana* group of *Mesomyia,* and by the occurrence of a species of *Vepriella* with perceptible hairs on its eyes in the south-eastern highlands (Fig. 12*A*).

If these differences are primarily adaptive to differences in local environment, as seems indicated, then it would follow that the bare-eyed Australian species may be more nearly related to the hairy-eyed species from the same country than to the bare-eyed African species. There are morphological indications that this may be so, and there is certainly evidence that the banded-eyed Australian *Vepriella* is more nearly related to local *Pseudotabanus* than to South American *Veprius.*

The broad distribution of the complex and its derivatives (Fig. 4) provides further evidence pointing in the same direction. There are three centres of radiation: a small, local one in South America; a much larger one in southern and eastern Africa, with one tongue (*Dasycompsa*) extending westward into the tropical rain-forest, and a second (*Aegophagamyia* and allies) eastward into the Malagasy subregion; and another large centre in Australia, with a single, westward extension (*Eucompsa*) into the Malay Archipelago. There is no evidence of a true Oriental fauna in this group, nor of any connection around the Indian Ocean between *Eucompsa* and the Malagasian genera.* Consequently, none of the Australian groups can be accepted unreservedly on present evidence as representing a separate northern element in the Australian fauna.

The most likely hypothesis at this stage of knowledge is that the *Dasybasis*-like and undistinguished species with perceptibly hairy eyes lie nearest to an originally widespread, southern ancestral stock, which has disappeared from southern Chile and Patagonia, but has persisted in southern Africa and southern Australia as *Mesomyia* (s.s.). In each region, this stock has given rise to smoother, relatively bare-eyed offshoots adapted to life in the warmer parts of the country. Thus, in Australia the northern distribution of these smoother species would indicate, not northern origin, but radiation into previously unoccupied territory, occurring at an earlier period than the massive Oriental invasion, typified by *Tabanus,* with which it could now be confused.

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* The two species of "*Silvius*" recorded from Ceylon by Szilàdy (1926) were inadequately described, but the characters given suggest that they were more likely to have been Chrysopini than Bouvieromyiini.

Accepting this hypothesis provisionally, it becomes the more desirable to give the different elements in the genus taxonomic recognition, provided reasonable morphological grounds exist for doing so. The characters available are not substantial, but I believe that there is sufficient conformity within the groups to justify their use. For practical reasons, the further limitation may be imposed that groups will be accepted as subgenera only when both sexes can be correctly placed.

Having accepted subgenera within what may be termed the core of the complex, the final question arises, where to draw the line between those offshoots that should be included as additional subgenera, and those that are regarded as sufficiently divergent to warrant full generic recognition. This decision can only be personal and arbitrary, depending on the weight the individual worker gives to particular characters. Looking at the tribe as a whole, *Merycomyia,* the *Aegophagamyia* group, *Pseudopangonia* and *Phibalomyia* probably would be accepted by all workers as generically distinct from *Mesomyia.* At the other end, *Bacloceras* (Oldroyd, personal communication) and *Pareucompsa* fall in reasonably as subgenera. That leaves four which might be recognized at either level, namely, *Rhigioglossa* (shining frons without callus, reduced antennal annuli), *Pronopes* (dichoptic eyes in ♂), *Dasycompsa* and *Eucompsa* (both with tomentose frons without callus and 3-annulate antennal style, but differing from each other in other respects). I feel that the salient characters indicated are sufficiently unusual in the tribe to justify acceptance of these four provisionally as separate genera, and they are treated accordingly in the present work. This course, as Mr. Oldroyd has pointed out to me, has the additional practical advantage that the well-known name *Mesomyia* will not be replaced by the earlier, little known *Rhigioglossa,* which, moreover, is attached to a small and aberrant element in the complex.

The subgenera will be defined fully under the appropriate regions, but their salient features may be summarized here in semi-tabular form, in order to show the scope of the genus as a whole and the kind of subgeneric characters relied on.

(A) *Eyes (in fresh or relaxed specimens) banded in both sexes*

Veprius: Eyes with hairs perceptible at ×15; subcallus and face shining; 1st antennal segment not expanded; *sc* setulose below; style of ♂ hypopygium without ventral lobe. Central Chile, adjacent Argentina.

Vepriella: Eyes usually bare; subcallus and face tomentose; 1st antennal segment usually expanded and hood-like dorsally (Fig. 11); *sc* setulose below; style of ♂ hypopygium with ventral lobe. Australia; ?New Guinea.

Pareucompsa: Style of 3rd antennal segment 3-annulate (4-annulate in all other subgenera); otherwise like *Vepriella*, except that 1st antennal segment is normal, *sc* bare, and wings usually with distinctive, *Chrysops*-like pattern. New Guinea.

(B) *Eyes unbanded in female, with a narrow band in male*

Lilaea: Eyes bare; subcallus shining; face tomentose; palpi of ♀ distinctive (Fig. 13); *sc* bare; style of ♂ hypopygium with attenuated tip. Australia.

(C) *Eyes unbanded in both sexes; subcallus and face tomentose*

Pseudotabanus: Eyes bare; 1st antennal segment not expanded (cf. *Vepriella*); *sc* almost always setulose below; style of ♂ hypopygium usually with ventral lobe; smooth, *Cydistomyia*-like species. Australia; New Guinea.

Perisilvius: Eyes bare or with barely perceptible hairs; *sc* bare; style of ♂ hypopygium without ventral lobe; undistinguished or *Cydistomyia*-like species. Southern and eastern Africa.

Mesomyia: Eyes distinctly hairy; *sc* setulose below or bare (always bare in African species); style of ♂ hypopygium without ventral lobe; usually more hairy, *Dasybasis*-like species. Southern and eastern Africa; Australia.

Bacloceras: Distinguished from *Mesomyia* by its peculiar, rod-like 3rd antennal segment; eyes hairy. South Africa.

This arrangement does not take account of the fact that there are two distinct groups in *Pseudotabanus*, one well defined and showing affinities with *Vepriella*, the other intermediate in some respects between *Pseudotabanus* and *Mesomyia*; and it may not provide adequately for the bare-eyed African species. It does, however, form a working basis, on which further improvement can be made.

The genera of the tribe may now be taken up serially by regions.

Nearctic

Genus MERYCOMYIA Hine, 1912

Genotype: *Merycomyia geminata* Hine, 1912 (= *Tabanus whitneyi* Johnson, 1904), Connecticut, by original designation.

Species examined.—*whitneyi* (Johns.), ♀, det. Philip by comparison with type.

Female

Bulky, *Tabanus*-like flies. Eyes unbanded; bare. Frons medium to wide (index 1.5 to 3), almost parallel, with an elongate or diamond-shaped callus. Subcallus moderately bulging, tomentose, without hairs.

Face flat, tomentose. Antennae short and wide; 1st segment large, expanded apically, about as long as width at apex; 2nd small; 3rd short and stout, with a rounded dorsal angle, and a short, plump, 3- or 2-annulate style. Palpi with 2nd segment short, considerably swollen basally. Proboscis very short; labella large and fleshy. Legs normal; hind tibial spurs very small, not detectable in the specimen before me. Wing with cells R_5 and M_3 open; vein *sc* bare, R_4 without appendix. Hypopygium: 8th sternite wide, and with a very shallow notch between gonopophyses, somewhat like the Australian *Pseudopangonia*; other parts normal.

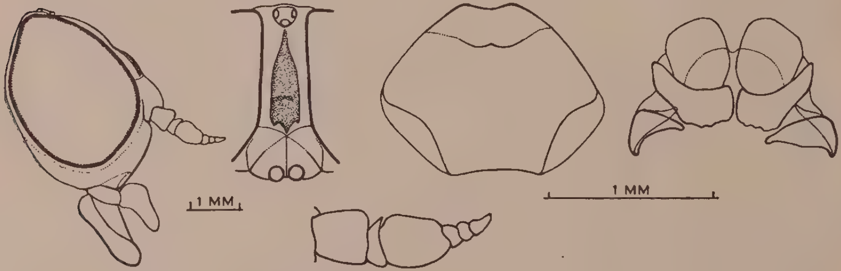

Fig. 5.—*Merycomyia whitneyi* (Johns.). (For caudal end of spermathecal duct, see Mackerras 1955, Fig. 2*G*.)

Distribution.—Four species from south-eastern United States and Haiti (Mackerras 1954, Fig. 9).

This genus is the only representative of the tribe in the northern hemisphere. It is undoubtedly correctly placed, but no "markers" appear to have been left to indicate the pathway that its ancestors must have followed.

Neotropical

Genus MESOMYIA Macquart, 1850

Subgenus VEPRIUS Rondani, 1863

Subgenotype: originally monotypic for *Veprius presbiter* Rondani, 1863, Chile.

Species examined.—*presbiter* (Rond.), ♂ ♀, det. Oldroyd and Philip.

Female

Eyes (relaxed) with a bright brown band on a dark green ground; with fine hairs perceptible at ×15. Frons median (index 3.3), slightly diverging; callus elongate club-shaped. Subcallus rounded, prominent, distinctly shining through thin tomentum, hairy at sides. Face shining through a trace of tomentum. First antennal segment not enlarged. Palpi firm and moderately slender, tapering to a rounded end. Proboscis strong. Vein *sc* setulose below. Genitalia: 8th sternite angular at sides;

caudal ends of spermathecal ducts moderately chitinized, and with a small but distinct annular swelling at the cranial end.

Male

Upper facets of eyes slightly enlarged. Palpi relatively long and slender, tapering somewhat to a rounded end. Genitalia: 9th tergite completely divided in mid-line, each half without indication of subdivision into a proximal and distal portion; style bluntly pointed, without ventral lobe; cerci bilobed apically.

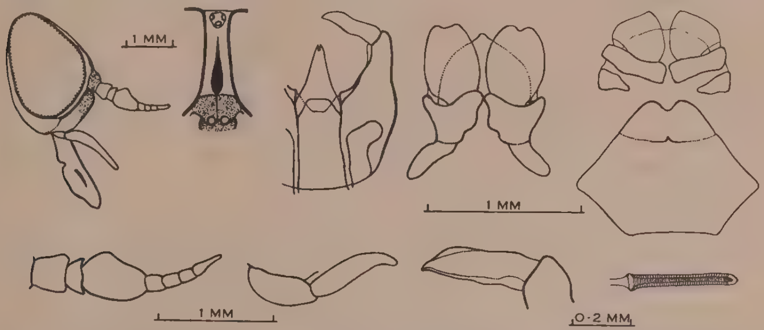

Fig. 6.—*Mesomyia* (*Veprius*) *presbiter* (Rond.). The bottom row, from the left, comprises antenna of female, palp of male, style of male hypopygium, and caudal end of a spermathecal duct of female.

Distribution.—Central Chile and Neuquén district of Argentina (Hack 1951).

The essential subgeneric characters are the banded eyes, which are only faintly hairy, shining subcallus and face, unenlarged 1st antennal segment, and broadly *Tabanus*-like habitus. The subgenotype is a medium sized, black species, with darkened wings.

*Ethiopian**

Genus MESOMYIA Macquart, 1850

Subgenus MESOMYIA Macquart, 1850

Pseudoscaptia Enderlein, 1922. Type *Pseudoscaptia scoliiformis* Enderlein, 1925 (=*Rhinomyza costata* Loew, 1860), South Africa, by original designation. Synonymy by Oldroyd (personal communication) from examination of the type of the genotype.

Species examined.—*schoutedeni* (Beq.), ♂♀, det. Austen as *fallax* Aust.

* Mr. Oldroyd has called my attention to a paper by Séguy (*Mem. Inst. sci. Madagascar* A3: 277-300, 1949), which I have not seen, and in which two genera of this tribe, *Rhinomyzopsis* and *Silviusopsis*, are described as new. They do not materially affect the present review, and will be dealt with in Oldroyd's third volume on the Ethiopian fauna.

Female

A medium sized, moderately hairy, *Dasybasis*-like species. Eyes unbanded; with short hairs visible at ×15. Frons wide (index 2), diverging; callus wide and short, without extension. Subcallus tomentose, without hairs. Face tomentose. First antennal segment not expanded; 3rd with sub-basal dorsal hump, giving it an unusual appearance (Fig. 7); style 4-annulate. Palpi swollen at base, tapering to a rounded point, and with a dorsolateral slit or scar. Vein *sc* bare. Caudal ends of spermathecal ducts moderately chitinized and of unusual shape, resembling those of *Dasycompsa*.

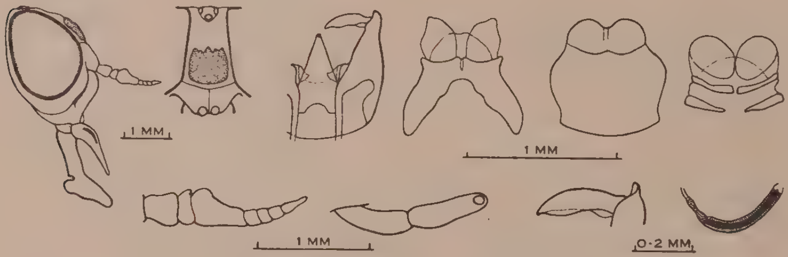

Fig. 7.—*Mesomyia* (*Mesomyia*) *schoutedeni* (Beq.).

Male

Eyes densely and obviously hairy; upper facets not markedly enlarged. Subcallus with some hairs at sides. Palpi subcylindrical, with a well-marked apical pit. Genitalia: 9th tergite incompletely divided in the mid-line, but of normal shape for the subfamily, the lateral halves without indication of partial subdivision into proximal and distal portions; style without ventral lobe.

Other species of the subgenus conform in general with this definition, except that the eyes of the females are more obviously hairy (Oldroyd, personal communication).

Distribution.—Southern and eastern Africa, with *schoutedeni* extending into the Katanga district of the Belgian Congo.

Subgenus PERISILVIUS Enderlein, 1922

Subgenotype: originally monotypic for *Perisilvius nyassicus* Enderlein, 1925, Nyasaland.

Species examined.—*monticola* (Neave), ♂ ♀, det. Austen and Oldroyd.

Mr. Oldroyd has informed me that *P. monticola* is close to *P. nyassicus*. It is a small, undistinguished species, which differs from *M. schoutedeni* in the following respects: hairs on eyes very short and fine in both sexes (barely perceptible at ×15); frons of ♀ with a linear callus; subcallus conspicuously hairy; 3rd antennal segment without strong dorsal hump;

palpi of ♀ short, soft, rather plump, without dorsolateral slit or scar, of ♂ short, rounded, and without apical pit; proboscis unusually short and soft; gonopophyses of ♀ strongly chitinized; caudal ends of spermathecal ducts pale, simple tubes.

Other species, including the subgenotype, have unequivocally bare eyes, and one or two are rather *Cydistomyia*-like, but all have a linear callus in the female. Mr. Oldroyd considers that the group may usefully be given subgeneric status in Africa, although it does appear to merge with *Mesomyia* through the Australian *montana* group of that subgenus.

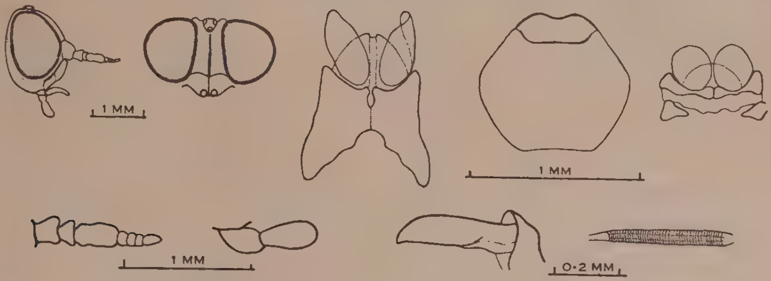

Fig. 8.—*Mesomyia* (*Perisilvius*) *monticola* (Neave).

Distribution.—Southern and eastern Africa.

Subgenus BACLOCERAS Austen, 1937

Subgenotype: monotypic for *Bacloceras turneri* Austen, 1937, Natal.

Mr. Oldroyd has informed me that *Bacloceras* is best treated provisionally as a subgenus of *Mesomyia*. The type ♂ is still unique, and it is distinguished only by the curious slender, rod-like 3rd antennal segment, which, however, was found to be composed basically of the normal 5 divisions. The eyes are densely hairy, and the 2nd segment of the palp, as figured by Austen (1937, p. 264), is quite like that of the Australian *M. cydister*.

Distribution.—South Africa.

Genus DASYCOMPSA Enderlein, 1922

Genotype: originally monotypic for *Dasycompsa cincta* Enderlein, 1925, Cameroons.

Species examined.—*apiformis* (Neave), ♀, det. Austen and Philip.

Female

Very hairy, bee-like flies. Eyes unbanded; densely haired. Frons almost square, tomentose, without callus. Subcallus tomentose, hairy. Face tomentose. Third antennal segment normally with a 3-annulate style.* Palpi swollen at base, slender apically, without dorsolateral scar, covered with long, silky hairs. Hind tibiae with a strong fringe of hairs. Vein *sc* bare. Hypopygium normal, except for the caudal ends of the spermathecal ducts, which are shorter than in *M. schoutedeni* but of the same unusual form.

This genus is close to *Mesomyia* (cf. Figs. 7 and 9), but may be distinguished by the absence of a callus, normally 3-annulate antennal style, and strikingly bee-like appearance. Its acceptance at higher than subgeneric rank is provisional.

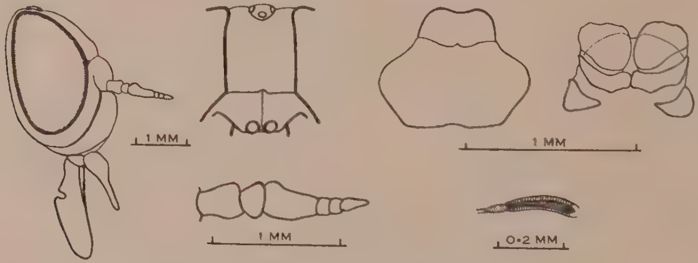

Fig. 9.—*Dasycompsa apiformis* (Neave).

Distribution.—Cameroons and Belgian Congo (*cincta*); Nyasaland (*apiformis*).

Genus PRONOPES Loew, 1858

Genotype: originally monotypic for *Pronopes nigricans* Loew, 1858, Cape of Good Hope.

Eyes hairy, separated in both sexes; frons index of ♀ less than 1; palpi short; proboscis short; hind tibial spurs minute; wings longer than whole body; abdomen very short and flat.

These notes are chiefly from Bequaert (1930). The genus is evidently close to *Mesomyia*, but widely separated eyes in the male is, so far as I know, a unique character in the tribe, so it may be allowed to stand.

Distribution.—South Africa (2 spp.).

Genus RHIGIOGLOSSA Wiedemann, 1828

Genotype: originally monotypic for *Rhigioglossa testacea* Wiedemann, 1828 (= *Rhinomyza edentula* Wiedemann, 1828), South Africa.

Erodiorhynchus Macquart, 1838. Monotypic for *Erodiorhynchus cristaloides* Macquart, 1838 (= *Rhinomyza edentula* Wiedemann, 1828).

Scarphia Walker, 1850. Monotypic for *Pangonia directa* Walker, 1850 (= *Rhinomyza edentula* Wiedemann, 1828).

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* Dr. Philip has sent me a specimen with the style of both antennae clearly 4-annulate.

Metoponaplos Ricardo, 1915. Monotypic for *Pangonia parva* Walker, 1848 (= *Rhinomyza edentula* Wiedemann, 1828).

The above synonymy is from Bequaert (1930).

Female

Eyes bare, widely separated. Frons entirely shining, without callus. Subcallus and face tomentose, to judge from Miss Ricardo's (1915) description. Basal plate of 3rd antennal segment wide, rounded dorsally; apical annuli small and more or less fused, so that the segment may show only 2 distinct annuli. Palpi broad at the base, and ending in a long, tapering point. Wing with cell R_5 occasionally closed, if Enderlein (1922) is correct.

Distribution.—South Africa (3 spp.).

Genus AEGOPHAGAMYIA Austen, 1912

Genotype: *Aegophagamyia pungens* Austen, 1912, Zanzibar, by original designation.

Species examined.—pungens Aust., ♂ ♀, det. Austen and Philip.

A small, slender, smooth species, immediately distinguishable from any of the preceding genera by havings cells R_5 and M_3 closed.

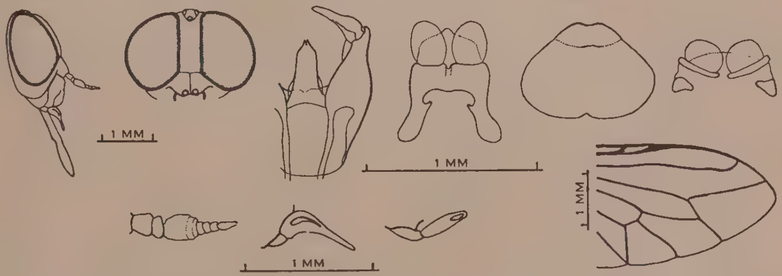

Fig. 10.—*Aegophagamyia pungens* Aust. Bottom series: antenna of female, palp of female, palp of male, wing of female.

Female

Eyes unbanded; with fine hairs just perceptible at ×15. Frons medium (index 3), slightly diverging, tomentose, without callus; ocellar tubercle rather flat. Subcallus tomentose, without hairs. Face tomentose. Antennae short; basal section of 3rd segment oval, no longer than the 4-annulate style. Palpi unusual, rather pangoniine-like, swollen basally, tapering apically, and with a deep dorsolateral groove. Proboscis relatively long and slender, with relatively long, narrow, firm labella. Vein *sc* bare; fused section of R_5 and M_1 long. Hypopygium: 8th sternite rather wide; caudal ends of spermathecal ducts pale, simple tubes, like those of *P. monticola*.

Male

Eyes with upper facets somewhat enlarged, but merging into the lower. Palpi shorter than in ♀, subcylindrical, with a dorsolateral bare area. Hypopygium: 9th tergite incompletely divided in the mid-line, otherwise normal.

Distribution.—About seven species from Kenya; Zanzibar; Madagascar; Rodriguez I.; Astove I.

Aegophagamyia, in spite of its venational specialization, is clearly related to the more generalized African members of the tribe, from which it must be regarded as an offshoot, rather than as a separate faunal element of independent origin. Its name is derived from the fact that all the specimens of the type species were taken feeding on goats.

Genus BOUVIEROMYIA, Strand, 1928

Nom. nov. for *Bouvierella* Surcouf, 1909, nec Chevreux, 1900.

Genotype: *Bouvierella notata* Surcouf, 1909, Madagascar, by designation of Enderlein, 1922.

Eyes bare. Frons with well-developed, elongate callus. Basal plate of 3rd antennal segment with a blunt dorsal tooth. Proboscis short and stout, with large labella. Cells R_5 and M_3 closed; fused section of R_5 and M_3 short. Bequaert (1930) noted that *B. inornata* (Aust.) has the proboscis and venation of *Aegophagamyia*, but the frontal callus of *Bouvieromyia*, and he doubted whether the relative lengths of the stalks of cells R_5 and M_3 were a reliable character.

Distribution.—As restricted by Bequaert, the genus contains only two species from Madagascar.

Genus TRICLIDA Enderlein, 1923

Genotype: *Triclida lurida* Enderlein, 1923, Madagascar, by original designation.

Stypotrichia Enderlein, 1923. Monotypic for *Bouvierella chopardi* Surcouf, 1913, Madagascar. Synonymy by Bequaert, 1930.

Trichidommisa Enderlein, 1923. Monotypic for *Trichidommisa hildebrandti* Enderlein, 1923, Madagascar. Synonymy by Bequaert, 1930.

Bequaert separated this group of species from typical *Bouvieromyia* on the basal plate of the 3rd antennal segment, which is evenly rounded dorsally and has no tooth. To judge from what happens in *Mesomyia* (and also in Diachlorini), this character seems unlikely to have even subgeneric value. If *Bouvieromyia* falls under *Triclida* (and possibly both under *Aegophagamyia*), we will have the unfortunate situation that the tribal name is based on a subjective synonym, but that seems to be unavoidable under the new Rules. Oldroyd is revising these genera, so no more need be said about them here.

Distribution.—Malagasy subregion: About 14 species from Madagascar, Seychelles, and Comoro I.

Genus DISCIONE Enderlein, 1934

Genotype: monotypic for *Discione syrphoides* Enderlein, 1934, Madagascar.

Genus APHOTRICLISTA Enderlein, 1934

Genotype: monotypic for *Aphotriclista madagascariensis* Enderlein, 1934, Madagascar.

Enderlein described these genera as Scionini, but Mr. Oldroyd has informed me that they both belong to the present section of the Bouvieromyiini. I can find nothing in the definitions, or descriptions of the type species, to distinguish them from *Bouvieromyia.*

Oriental

Genus EUCOMPSA Enderlein, 1922

Genotype: originally monotypic for *Eucompsa aureocincta* Enderlein, 1925, Java.

Apparently differs from the Australasian *Pareucompsa* only in lacking a callus, and retained here as distinct for much the same provisional reason as *Dasycompsa* in the Ethiopian region.

Distribution.—One species from Java and one from Borneo (Schuurmans Stekhoven 1932).

Australasian

Genus MESOMYIA Macquart, 1850

As the arrangement presented here is new, the species included will be listed in full under each subgenus.

Subgenus VEPRIELLA, subgen. nov.

Subgenotype: *Silvius frontalis* Ricardo, 1915, Northern Territory, by present designation.

Species included.—frontalis (Ric.), ♀; *indistincta* (Ric.), ♀; *insularis* (Ric.) ♀; *equina* (Ferg. & Hill), ♀; 4 undescribed spp. or subspp. (♀♀ of 4, ♂♂ of 2); possibly *lunulata* (Big.); possibly *vittata* (Ric.).

Usually small to medium sized, smooth, *Tabanus*-like species, with clear to somewhat smoky wings.

Female

Eyes with 1 or 2 bright blue to green bands on a dark brown or blackish ground; usually bare. Frons medium to narrow (index 2.5 to 4), usually converging; callus nearly always quadrate and full width of frons at base, with a narrow median extension. Subcallus flat, tomentose, occasionally (*frontalis*) with strong hairs. Face tomentose. First antennal segment usually enlarged and hood-like dorsally (Fig. 11); 3rd with 4-annulate style. Palpi firm, slender, rounded at tip. Proboscis strong. Vein *sc* setulose below. Genitalia: gonopophyses large, separated by a shallow notch; caudal ends of spermathecal ducts slender, moderately chitinized, simple tubes.

Male

Eyes with upper facets considerably or slightly enlarged. Palpi short, subcylindrical, tapering distally to a rounded point. Genitalia: 9th tergite completely divided in mid-line, and each half more or less distinctly divided into proximal and distal portions; style more slender than in *Veprius,* and produced below into a projecting subapical ventral lobe (seen in dorsal view as an oval clear area near tip of style).

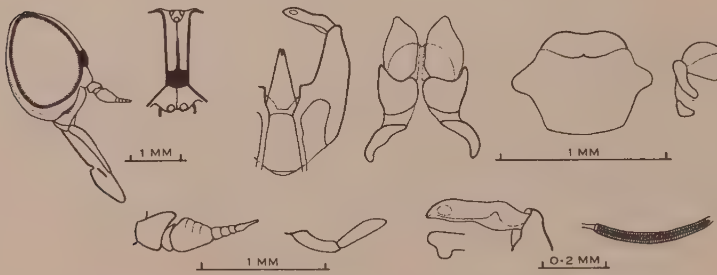

Fig. 11.—*Mesomyia* (*Vepriella*) *frontalis* (Ric.), female, and sp. nr. *indistincta* (Ric.), male. The inset below the style is a diagrammatic representation of its ventral lobe, as seen in lateral view.

Distribution.—North-western Australia (1 sp.); Northern Territory (3); north Queensland (1); New South Wales (1); south-western Western Australia (1); *vittata* (Ric.) from New Guinea, probably also belongs here, although the callus is not quadrate at base.

Vepriella is clearly derived from the *Pseudotabanus* stock, and is easily recognized in Australia, not only by the eye pattern, but by the shape of the 1st antennal segment. An interesting point of contrast (among others) with *Veprius* is that the eye pattern is reversed, brown on green in *Veprius,* green or blue on brown in *Vepriella.*

The species from the Blue Mts. in New South Wales differs from the others in being larger, darker, more hairy, and having eyes perceptibly hairy at ×15. It provides significant supporting evidence for the hypothesis that these characters are influenced by climate, because its relationships are perfectly clear.

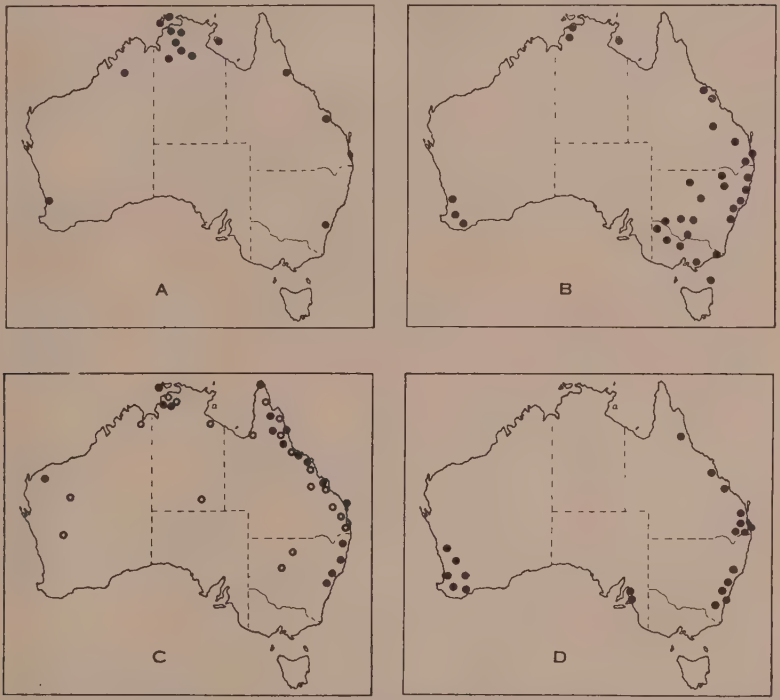

Fig. 12.—Distribution of Australian subgenera of *Mesomyia*. *A*, *Vepriella*; *B*, *Lilaea*; *C*, *Pseudotabanus* (solid dots *distincta* group, circles *australis* group); *D*, *Mesomyia*.

Subgenus PAREUCOMPSA Enderlein, 1922

Subgenotype: *Silvius dimidiatus* van der Wulp, 1868, New Guinea, by original designation.

Species included.—dimidiata (Wulp); *femoralis* (Ric.); possibly *atrata* (S.S.).

I have not seen this subgenus, which has been reviewed by Oldroyd (1947).

Female

Eyes with a green band in life; bare. Frons of genotype converging, index 2.5; callus club-shaped (Oldroyd 1947, Fig. 8). Subcallus and face tomentose. First antennal segment not enlarged; style of 3rd with *3* annuli. Palpi similar to *Pseudotabanus*. Wing usually with a *Chrysops*-like, dark pattern. The antennal style is 3-annulate only as an occasional individual aberration in other Australasian subgenera.*

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* See Addendum, p. 633.

Distribution.—New Guinea.

It may appear inconsistent to accept a 3-annulate antennal style as of generic value in *Dasycompsa* and *Eucompsa,* but not here. However, they are distinguished in other ways also, particularly by the absence of a callus, whereas *Pareucompsa* is not. Moreover, they may both end as subgenera of *Mesomyia,* when more is known about them.

Subgenus LILAEA Walker, 1850

Subgenotype: *Pangonia lurida* Walker, 1848, Australia, by designation of Coquillett, 1910.

Species included.—lurida (Walk.), ♀; *paralurida* (Ferg. & Henry), ♀; *stradbrokei* (Tayl.), ♀; *abra* (Philip)*, ♂ ♀; *mansoni* (Summers), ♀.

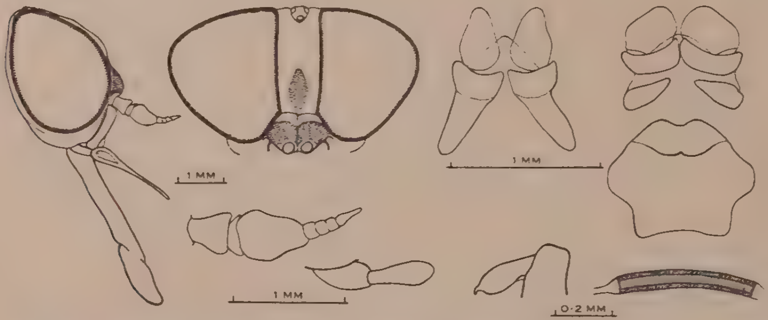

Fig. 13.—*Mesomyia* (*Lilaea*) *lurida* (Walk.), female, and *abra* (Philip), male.

This genus was misunderstood by Enderlein (1922, 1925), who chose *roei* Macleay as genotype in ignorance of Coquillett's prior action, and thus brought it into *Scaptia* (*Pseudoscione*) as defined in Part II (Mackerras 1955). Ferguson (1924) selected the same genotype as Coquillett, and reduced it to synonymy of *Silvius* s.l. Oldroyd (1947) clarified the synonymy, and resurrected the name for Australasian species which had been described as *Silvius.* It is used here in a more restricted sense.

Medium sized to large, smooth, *Tabanus*-like flies, with clear wings.

Female

Eyes unbanded; bare. Frons medium (index 2.5 to 3.5), converging; callus small, narrower than frons and restricted to its lower half, sometimes inconspicuous. Subcallus prominent, shining, sometimes highly polished, without hairs. Face tomentose. First antennal segment not enlarged. Palpi (Fig. 13) characteristic, very long, tapering, flattened, and with a well-defined lateral bare area near the widened base. Proboscis strong. Vein *sc* bare. Genitalia: 8th sternite and gonopophyses undistinguished; caudal ends of spermathecal ducts larger and more prominent than in other subgenera, straight-sided, simple tubes without expansions.

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* Better known as *notata* (Ric.).

Male (abra *only*)

Eyes very large; with a narrow blue-green band at junction between the conspicuously enlarged upper and small lower facets. Palpi short and plump, rounded apically. Genitalia: 9th tergite completely divided and of somewhat distinctive shape; style tapering to a hooked point and without ventral lobe; cerci rounded apically.

Distribution.—North-western Australia, Northern Territory, and north Queensland (2 spp.); south Queensland and New South Wales (4); Victoria (2); south-western Western Australia (2). Some species occur in more than one zone.

Lilaea appears to be an essentially Australian development, with no near relatives elsewhere. It is the most easily recognizable of the subgenera, its salient features being the bare eyes, shiny subcallus, characteristic palpi of the female and absence of setulae on *sc*. No intermediate or doubtful species have been seen.

Full grown larvae of *L. abra* were found by Johnston and Bancroft (1920) in muddy sand at the edge of the Burnett River. and by Hill (1921) in nearly dry soil about 12 ft from a small lily-pond at Townsville. It seems likely that the younger stages may be aquatic (?demersal). The larva (Mackerras 1955, Fig. 3) has the typical posterior spike, like *Chrysops*, but the pupa has a lateral comb on the 8th abdominal segment, short antennal sheaths, and is apparently to be distinguished from pupae of *Dasybasis* (Diachlorini) only by comparatively minor details of chaetotaxy (Miss English, personal communication).

Subgenus PSEUDOTABANUS Ricardo, 1915

Subgenotype: *Pseudotabanus distinctus* Ricardo, 1915, north Queensland, by designation of Enderlein, 1925.

Species included.—*distincta* group: *distincta* Ric., ♀; *queenslandi* Ric., ♀; *distincta* (Tayl.)*, ♀; *fuscipennis* (Ric.), ♀; *grandis* (Ric.), ♀; *ater* (Tayl.), ♂ ♀; *nigripennis* (Ric.), ♂ ♀; *fergusoni* (Ric.), ♂ ♀; *demeijerei* (Ric.), ♀. *australis* group: *australis* (Ric.), ♂ ♀; *alcocki* (Summers), ♀; *marginata* (Walk.), ♀; 2 undescribed spp. (♀ of both); *atriventer* (S.S.) from New Guinea probably also belongs here.

This subgenus was misunderstood by Enderlein (1922, 1925) and Kröber (1931). It is not pangoniine but chrysopine, as Ferguson (1926) in effect pointed out, and the subdivision of the basal plate of the 3rd

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* A new name will be proposed for this species in a forthcoming revision of the Australian Tabanidae.

antennal segment, which is often seen in the genotype and a few other species, is never more than incipient.

Large to small, smooth, *Cydistomyia*-like or slender species.

Female

Eyes unbanded; bare. Frons narrow to wide, converging or diverging; callus nearly always club-shaped. Subcallus flat, tomentose, with or without fine hairs at sides. Face tomentose. First antennal segment not enlarged. Palpi medium to slender, firm, rounded apically (as in *Veprius* and *Vepriella*). Proboscis strong. Vein *sc* almost always setulose below (except *demeijerei*). Genitalia as in *Vepriella*, except that the 8th sternite is more rounded laterally and the gonopophyses more clearly separated.

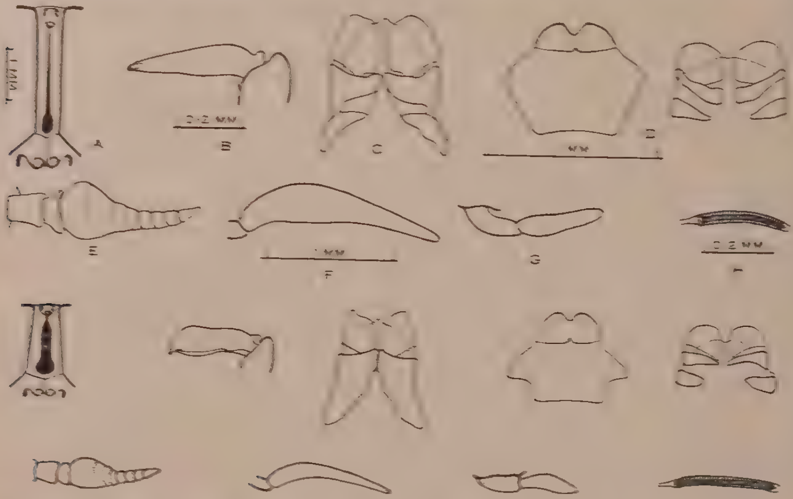

Fig. 14.—*Mesomyia*, subgenus *Pseudotabanus*. Upper series, *distincta* group: *A*, *fergusoni* (Ric.); *B*, *C*, *nigripennis* (Ric.); *D*, *E*, *F*, *H*, *distincta* Ric. (for head see Fig. 3*C*); *G*, *ater* (Tayl.).
Lower series, *australis* group: all *australis* (Ric.) at same magnifications as above.

Male

Upper facets of eyes slightly to considerably enlarged. Palpi and genitalia vary in the groups (q.v.).

Distribution.—See under groups (p. 609).

The subgenus contains two very distinct groups, which I would be inclined to treat as separate subgenera, were it not for the fact that the known males can only be distinguished by size and the shape of the hypopygial style. I have not sufficient confidence in either character to accept it as of subgeneric value in the present state of our knowledge.

The distincta *Group*

Frons of ♀ narrow (index more than 3.5), converging to parallel; callus elongate, Indian club-shaped. Palpi and genitalia of ♂ as in *Vepriella*. Large to medium sized species, with the wings nearly always darkened, at least anteriorly.

Distribution.—New Guinea (1 sp.); north-western Australia (1); Northern Territory (2); north Queensland (4); eastern coastal from Frazer I., south Queensland, to Sydney, New South Wales (1). No more typically "Oriental" distribution could be recorded, but reasons have been given earlier for considering this group to be probably a purely Australian development.

The australis *Group*

Frons of ♀ wide to medium (index 2 to 3), diverging to parallel; callus wider than in *distincta* group, irregularly club-shaped, occasionally anchor-shaped. Palpi of ♂ (*australis* only) short, conical, tapering to a rounded point. Lateral halves of 9th tergite of ♂ without trace of subdivision into proximal and distal portions; style stout, sharply pointed, without ventral lobe. Small, usually slender species, with clear wings.

Distribution.—New Guinea (?1 sp.); Northern Territory (3); north Queensland to western New South Wales and northern South Australia (1); south-western Western Australia (1).

This group is difficult to place. Most of its characters suggest relationship here, but the frons of the female and the palpi and 9th tergite of the male are rather *Mesomyia*-like, and the style of the male hypopygium is more like that of *Veprius* than any other Australian species examined.

Taylor (1917) described the eggs of *P. australis*, which he found on a blade of grass overhanging a small, sandy creek just as the fly had finished laying them. The mass, which is still preserved, is very long and narrow, about 27 mm long by 1.5 to 2 mm wide and 1 mm thick. It seems to consist of a closely packed bottom row laid very obliquely and a smaller top row laid flat on these. The individual eggs are now collapsed, but were described by Taylor as light amber-brown in colour, cylindrical, pointed like a cigar at the apex, and measuring about 1.3 by 0.2 mm.

Subgenus MESOMYIA Macquart, 1850

For taxonomic details, see pp. 591, 597.

Species included.—*doddi* (Ric.), ♂ ♀; *montana* (Ric.), ♀; *niger* (Ric.), ♂ ♀; *sulcifrons* (Ferg.), ♂ ♀; *tepperi* (Ferg.), ♀; *cydister* (Tayl.), ♂ ♀; *imitator* (Ferg.), ♂ ♀; and 2 undescribed spp. (♂ ♀ of one, ♀ of other).

Medium sized to small, usually hairy, often *Dasybasis*-like species, immediately recognizable in Australia by having unbanded eyes which are distinctly hairy at ×15. There is a gradation from the dense, conspicuous hairs on the eyes of *cydister* to the short, fine ones of *doddi*, but then a definite break, which collecting has not so far bridged, to the unequivocally bare eyes of *Pseudotabanus*.

Female

Frons wide to medium (index 2 to 3.5), usually diverging, occasionally parallel; callus linear, or irregularly club-shaped, or wide and short with a median extension. Subcallus tomentose, usually hairy. Face tomentose. First antennal segment occasionally swollen (*cydister*), but not hood-like dorsally; 3rd variable (Fig. 15). Palpi variable (even within species) from *Veprius*-like to relatively short, plump and soft, occasionally spatulate; usually more hairy than in other subgenera; without dorsolateral scar. Proboscis usually strong. Vein *sc* usually setulose below, sometimes bare. Caudal ends of spermathecal ducts usually short, pale, simple tubes, occasionally longer and moderately chitinized as in *Pseudotabanus*.

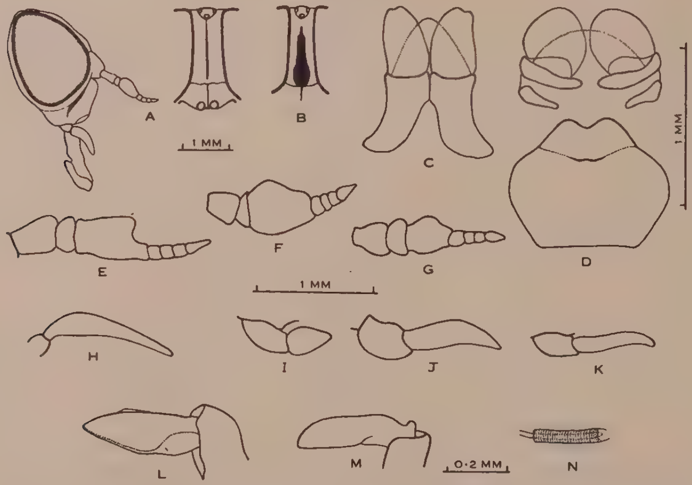

Fig. 15.—*Mesomyia*, subgenus *Mesomyia*, illustrating range of variation in Australian species. *A*, *montana* (Ric.) (for head of *cydister* see Fig. 3*A*); *B*, *G*, *tepperi* (Ferg.); *C*, *D*, *J*, *L*, *niger* (Ric.); *E*, *sulcifrons* (Ferg.); *F*, *K*, *imitator* (Ferg.); *H*, slender form of palp of female *montana*; *I*, *M*, *N*, *cydister* (Tayl.). Antennae *E*-*G* are of females, palpi *I*-*K* of males.

Male

Eyes with upper facets slightly to considerably enlarged. Palpi variable, but usually wider, more conical and more pointed at tip than in other subgenera; without detectable apical pit. Genitalia: 9th tergite completely divided in mid-line, occasionally showing indications of partial subdivision into proximal and distal portions; style without ventral lobe.

Distribution.—Eastern highlands, with coastal extensions, from north Queensland to Victoria (4 spp., possibly really subspp.) ; South Australia (2) ; south-western Western Australia (3).

I have no doubt that all the Australian species are properly included in a single subgenus, and have given the above definition in some detail to facilitate comparison with African species. The chief points of difference are: incomplete division of the 9th tergite of the ♂ and absence of setulae on *sc* in both African species studied (and also in *Aegophagamyia*, suggesting a general trend in that region) ; the peculiar palpi and spermathecal ducts of *M. schoutedeni*; and the less hairy eyes and chitinized gonopophyses of *P. monticola*. In other respects *M. schoutedeni* is quite like *M. cydister* and *P. monticola*, strikingly like *M. montana*.

Genus PHIBALOMYIA Taylor, 1920

Nom. nov. for *Elaphromyia* Taylor, 1917, nec Bigot, 1859.

Genotype: monotypic for *Elaphromyia carteri* Taylor, 1917, north Queensland.

Species examined.—carteri (Tayl.); ♂.

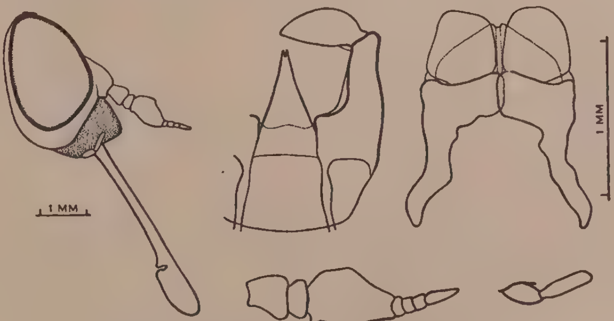

Fig. 16.—*Phibalomyia carteri* (Tayl.).

A rare insect, known only from the holotype in the School of Public Health and Tropical Medicine, Sydney, and two other males in the British Museum. Superficially it is very distinctive, as it is long and slender, with rather wasp-like colouration and markings.

Male

Eyes unbanded; bare; touching in mid-line, with some frontal hairs showing between them; upper facets not enlarged. Subcallus moderately bulging, tomentose, with hairs on each side. Face triangularly produced at middle, of rather peculiar shape, shiny. Antennae *Pseudotabanus*-like. Palpi very short, 2nd segment about equal to 1st, subcylindrical, with a dorsal bare area, and fairly strong hairs. Proboscis rather slender, a little longer than head height; labella expanded, firm, but apparently not chitinized. Legs long and rather slender; hind tibial spurs long. Wing with vein *sc* bare, R_4 without appendix; cell R_5 somewhat narrowed, M_3 widely open. Hypopygium: normal, except for the style, which is markedly expanded to an almost half-moon shape (Fig. 16), and sets the genus apart from its relatives.

Distribution.—North Queensland.

Genus PSEUDOPANGONIA Ricardo, 1915

Genotype: monotypic for *Pseudopangonia australis* Ricardo, 1915, south Queensland.

Species examined.—australis Ric., ♀.

Female

A large, inflated, soft-bodied, dull coloured insect, with an unusually small head. Eyes unbanded; bare. Frons narrow (index 5), parallel, longitudinally wrinkled, tomentose, without callus. Subcallus moderately bulging, tomentose, without hairs. Face hollow, with very large and deep tentorial pits, tomentose, and unusual in being practically without hairs. Antennae (Fig. 17) greatly modified; 1st segment inflated, a little longer than wide; 2nd cup-shaped; 3rd little more than half as wide as 2nd; its basal section is evenly swollen and awl-like, and the style is slender, truncate, and consists of 2 annuli and an indication of a 3rd. There is a remarkable resemblance to the antenna of *Asaphomyia* (Part II of this series, Fig. 10). Palpi nearly as long as the very short proboscis, tapering to a rounded point, rather soft and hairy; labella soft, and apparently without chitinous plates. Legs rather long, moderately stout; hind tibial spurs small. Wing with vein *sc* setulose below, R_4 without appendix; cells R_5 and M_3 open. Hypopygium rather broad and flattened, otherwise normal.

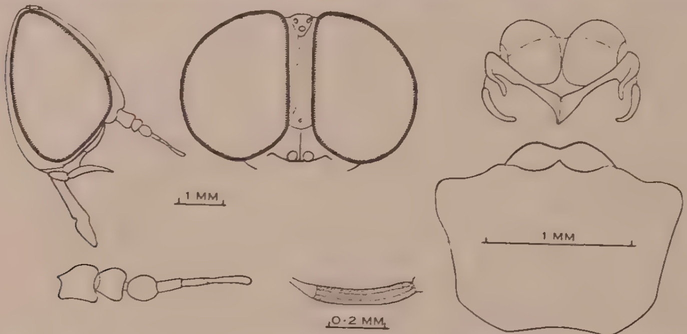

Fig. 17.—*Pseudopangonia australis* Ric. The antenna is from a cleared specimen.

Distribution.—Coastal districts of south Queensland and northern New South Wales.

Tribe CHRYSOPINI (Lutz, 1905)

Eyes bare; spotted, variegated, or freckled in life. Frons wide, index less than 2; callus large, transverse or rounded. Subcallus small. Face truncate or moderately bulging, often of characteristic shape in profile; nearly always with shining areas, which are occasionally reduced to a shining rim around tentorial pits, rarely absent. Antennae longer than antero-posterior thickness of head, usually much longer; 1st segment markedly longer than wide; 3rd usually slender and without defined dorsal hump, style always 4-annulate; any or all of the segments may show secondary annulations. Palpi of ♀ fusiform or spatulate, occasionally thickened, sometimes shining. Wing with vein sc bare, R_4 sometimes with appendix; cells R_5 and M_3 open, Cu_1 frequently open. Genitalia of ♂ and ♀ without distinctive features. Small, usually slender flies; cosmopolitan, but more generalized species almost exclusively Holarctic.

This tribe presents two main problems. The first is to make a clear distinction between it and Bouvieromyiini. *Silvius* is the difficulty, because the antennae are transitional, and the body of the genotype is not particularly slender. Three facts help. One is that the eyes of Chrysopini are distinctly spotted or mottled when alive or relaxed, whereas they are concolorous, or sometimes banded, in all the Bouvieromyiini I have examined. The second is that the comparatively few Bouvieromyiini with a wide frons and broad callus also have unequivocally short antennae and the eyes nearly always hairy. The third is that *Silvius* and Bouvieromyiini are not known to mix geographically. The only overlap is in the Nearctic region, where *Merycomyia* is very distinctive in appearance and eastern in distribution, whereas *Silvius* is western.

The second problem is to distinguish the genera. It is the recurrent difficulty, already mentioned several times, that typical members of, in this case, *Silvius* and *Chrysops* are easy to distinguish, but there are transitional forms which are difficult to classify. Thus, Enderlein (1922) and Séguy (1926) placed *Nemorius* near *Silvius*, the latter even including one of the two species (*singularis* Mg.) in *Silvius*; Bequaert (1930) regarded it as a synonym of *Chrysops*, and Kröber (1939) as a subgenus of *Chrysops*. Philip (1941*b*) erected the subgenus *Zeuximyia* for *Silvius philipi* Pech., which has *Chrysops*-like antennae (Fig. 18*B*), but is a *Silvius* in other respects. Conversely, *Chrysops hirsuticallus* Philip has antennae (Fig. 20*F*) which are more like a *Silvius* than a *Chrysops*. This difficulty at least emphasizes the fact that we are dealing with a compact group, and justifies Philip in his refusal to separate *Silvius* tribally from *Chrysops*. I have not been able to resolve this problem, and can only treat the genera conservatively here.

As only *Chrysops* is widely distributed, the genera may be dealt with more conveniently in a single series than by regions.

Genus SILVIUS Meigen, 1820

The only consistent character I can find to separate *Silvius* from *Chrysops* is the one used by Philip (1947, 1954) in his keys to the Nearctic genera, namely, that the eyes of *Silvius,* in life or relaxed, are freckled with small round spots, whereas in *Chrysops* the spots are large and angular. I therefore propose to treat the three described groups with small round spots as subgenera of *Silvius.*

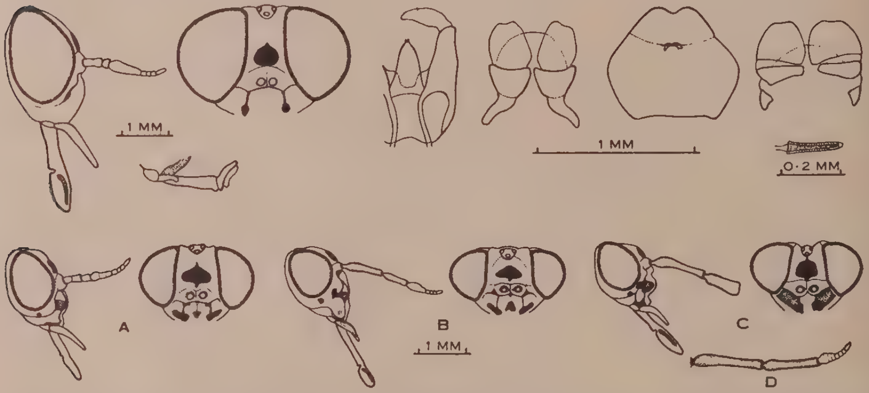

Fig. 18.—Upper series: *Silvius* (*Silvius*) *vituli* (Fabr.), female, and *gigantulus* (Loew), male (the inset to the left is the proboscis and palp of the male). *A, Silvius* (*Silvius*) *quadrivittatus* (Say); *B, Silvius* (*Zeuximyia*) *philipi* (Pech.); *C, Silvius* (*Assipala*) *tanycerus* (O.-S.); *D, S.* (*A.*) *melanoptera* Hine, antenna of female.

Subgenus SILVIUS Meigen, 1820

Subgenotype: originally monotypic for *Tabanus vituli* Fabricius, 1805, Europe.

Species examined.—Palaearctic: *vituli* (Fabr.), ♀, det. Szilàdy. Nearctic: *gigantulus* (Loew), ♂ ♀ ; *quadrivittatus* (Say), ♂ ♀ ; both det. Philip.

S. vituli and *S. gigantulus* are closely related, but *S. quadrivittatus* belongs to a rather distinct group of species which it will be convenient to define separately.

The vituli *Group*

Species of medium build, with clear wings and yellowish abdomen.

Female

Frons moderately wide (index about 1.5), slightly diverging, tomentose; ocellar tubercle tomentose or bare; callus rounded or heart-shaped. Subcallus tomentose, without hairs. Face rounded, mostly tomentose, but shining at sides at least around mouths of tentorial pits. Antennae relatively short, but still appreciably longer than antero-posterior

diameter of head; 1st segment about twice as long as wide; 2nd less than half as long as 1st; 3rd twice as long as 1st and 2nd together, slender, its basal section gently rounded dorsally and sometimes with vague indications of subdivision. Palpi spatulate, somewhat widened basally, rounded at tip, tomentose and with short hairs. Proboscis short, moderately stout; labella large, soft, with a narrow lateral chitinized band. Legs normal; fore tibiae not inflated. Wings with cell Cu_2 closed; vein R_4 with or without appendix. Genitalia: 8th sternite moderately wide, with a shallow concavity between gonopophyses; 9th tergal plates rather small and weak; caudal ends of spermathecal ducts short, pale, wider basally than distally.

Male

Eyes large, meeting in mid-line; upper facets distinctly enlarged. Antennae more slender than in ♀. Palpi short; 1st segment swollen; 2nd about twice as long as 1st, broadly cylindrical, rounded at apex. Genitalia: aedeagus small, smooth; flagella well developed; style broader than in *Chrysops*.

The quadrivittatus *Group*

More slender, greyish species, with the wings usually flecked with brown, and the abdomen with a somewhat *Chrysops*-like pattern. Additional points of distinction shown by *S. quadrivittatus* are: frons and callus wider (Fig. 18*A*); subcallus hairy in most specimens;* face longer and with shiny spots; antennae relatively longer; proboscis more slender, labella smaller and firmer; vein R_4 often angulate but without appendix, cell R_4 relatively short and wide; genitalia of both sexes rather more like those of *Chrysops* (Fig. 20), except that the caudal ends of the spermathecal ducts of the ♀ are not as slender.

This group leads through *Zeuximyia* to *Assipala*. These are more *Chrysops*-like, but their development would seem to have been parallel to that of *Chrysops* rather than in the direct line of its evolution.

Distribution (Fig. 19).—Palaearctic and northern Oriental: about 14 species from northern and southern Mediterranean, southern and central Europe, southern Russia, Caucasus, Persia, Afghanistan, northern India, Japan and Formosa. Nearctic: seven species and one subspecies from the southern and western United States, with an eastern limit in Illinois, Iowa, and Minnesota, and extending north on the western side into British Columbia. Szilàdy (1926) described two species of "*Silvius*" from Ceylon. As mentioned earlier, they may be Chrysopini, but the descriptions suggest that they probably do not belong to *Silvius* as defined here.

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* Hairs are present on the subcallus in three of the five American species of this group, whereas in *Chrysops* they were only found occasionally in the North American *C. hirsuticallus* and the Chilean *C. trifaria* (Philip, personal communication).

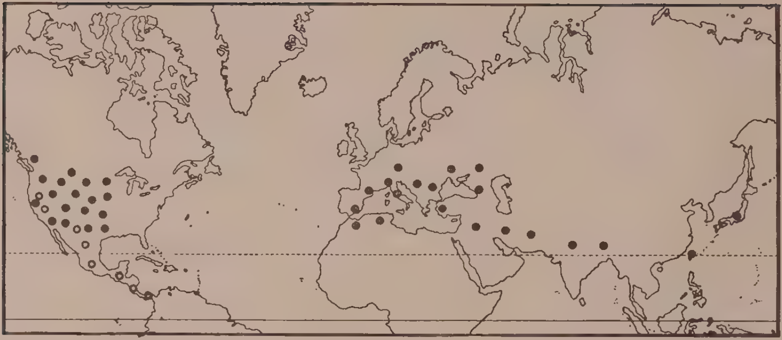

Fig. 19.—Distribution of the genus *Silvius*. Solid dots, subgenus *Silvius;* circles, subgenera *Zeuximyia* (northern) and *Assipala* (southern).

Subgenus ZEUXIMYIA Philip, 1941

Subgenotype: monotypic for *Silvius philipi* Pechuman, 1938, Oregon.

Species examined.—philipi Pech., ♀, det. Philip.

Female

Generally resembles *S. quadrivittatus,* and also has hairs on the subcallus; but distinguished by more slender build and long, *Chrysops*-like antennae (Fig. 18*B*). The palpi were described as slender, but they are somewhat widened in the specimen before me, and show indications of a longitudinal groove similar to that described in some members of the *quadrivittatus* group (Philip 1954).

Distribution.—Nearctic: Oregon and northern California.

Subgenus ASSIPALA Philip, 1941

Subgenotype: *Chrysops tanycerus* Osten-Sacken, 1886, Costa Rica, by original designation.

Species examined.—tanycerus (O.-S.), ♀, det. Philip; *melanoptera* (Hine), ♀, det. Fairchild.

Female

This subgenus shows additional *Chrysops*-like features. Slender species, with square frons and wide callus; ocellar tubercle prominent, tomentose; subcallus hairy at sides. Antennae (Fig. 18*D*) distinguished by the unusually short 3rd segment relative to the very long 1st and 2nd. Palpi *Silvius*-like. Wings spotted or darkened; vein R_4 evenly curved and without appendix; cell R_4 relatively short and wide; cell Cu_2 closed. Genitalia similar to *S. quadrivittatus,* but the caudal ends of the spermathecal ducts are more slender.

Distribution.—Southern Nearctic and northern Neotropical: four species from New Mexico, Mexico, Guatemala, Costa Rica, and Panama.

The final status of the *quadrivittatus* group and these two subgenera cannot be assessed until the Palaearctic species have been re-examined.

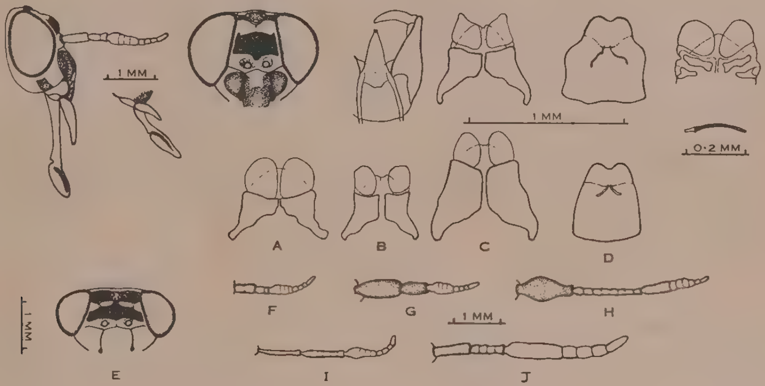

Fig. 20.—Upper series: *Chrysops caecutiens* (Linn.). *A, D, J, C. australis* Ric.; *B, E, G, C. laniger* Loew; *C, F, C. hirsuticallus* Philip; *H, C. austeni* Neave; *I, C. dispar* Fabr. The antennae are from females.

Genus CHRYSOPS Meigen, 1803

Genotype: originally monotypic for *Tabanus caecutiens* Linnaeus, 1758, Europe.

Chrysopsis Dumeril, 1806. Type *Tabanus caecutiens* Linnaeus, 1758, Europe, by designation of Philip, 1942.

Nemorius Rondani, 1856. Monotypic for *Chrysops vitripennis* Meigen, 1820, Europe.

Haemophila Kriechbaumer, 1873. Monotypic for *Haemophila fallotti* Kriechbaumer, 1873, (=*Chrysops vitripennis* Meigen, 1820), Europe.

Neochrysops Walton, 1918. Monotypic for *Neochrysops globosus* Walton, 1918, Maryland, U.S.A.

Heterochrysops Kröber, 1920. Type *Chrysops flavipes* Meigen, 1804, Europe, by designation of Bequaert, 1924.

Neochrysops Szilàdy, 1922, nec Walton, 1918. Monotypic for *Neochrysops grandis* Szilàdy, 1922, Formosa.

Ziemannia Enderlein, 1923. Monotypic for *Chrysops laniger* Loew, 1860, South Africa.

Kleineana Enderlein, 1923. Type *Chrysops longicornis* Macquart, 1838, Africa, by original designation.

Psylochrysops Szilàdy, 1926, nom. nov. for *Neochrysops* Szilàdy, 1922, nec Walton, 1918.

Turanochrysops Stackelberg, 1926. Monotypic for *Chrysops* (*Turanochrysops*) *hyalipennis* Stackelberg, 1926, Trans-Caspian.

Liochrysops Philip, 1955. Monotypic for *Chrysops hyalina* Shannon, 1924, Maryland, U.S.A.

Subgenera accepted by various authors are, for convenience of recording, listed here as synonyms.

Species examined.—Palaearctic: *caecutiens* (Linn.), ♂ ♀; *rufipes* Meig., ♂; both det. Szilàdy. Nearctic: *aberrans* Philip, ♂ ♀; *dacne* Philip, ♀; *discalis* Willist., ♂ ♀; *furcata chagnoni* Philip, ♀ : *hirsuticallus* Philip, ♂ ♀; *hyalina* Shan., ♀; *latifrons* Bren., ♀; all det. Philip. Neotropical: None. Ethiopian: *laniger* Loew, ♂ ♀; *silacea* Aust., ♀; both det. Oldroyd; *austeni* Neave, ♀, det. Austen. Oriental: *flaviventris* Macq., ♀; *fixissima* Walk., ♀; *dispar* Fabr., ♀; *translucens* Macq., ♀; all det. I.M.M. Australasian: ?*albicincta* Wulp, ♀; *australis* Ric., ♂ ♀.

A generally well-defined genus of small, relatively slender flies, with large angular spots or variegated dark markings on the eyes, long antennae, and usually banded wings. It stands out sharply in every fauna except the Holarctic.

Female

Frons very wide, index 0.7 to 1.3; callus large, broadly oval or transverse; ocellar tubercle also frequently shiny. Subcallus short but wide, nearly always without hairs. Face usually smoothly bulging in characteristic form, and almost always (except *C. laniger*) with more or less extensive shiny areas, which sometimes project forwards. Antennae often as long as head and thorax together, the segments of very variable relative length, and frequently with subsidiary annulations. Palpi usually smoothly fusiform and somewhat shining, sometimes indistinguishable from those of *Silvius*, occasionally (*C. discalis*) with a longitudinal cleft. Proboscis relatively slender; labella small, firm, and with more or less well-developed lateral chitinous band. Legs: fore coxae longer than usual and tibiae often slightly swollen, so that the front legs have a somewhat raptorial appearance; hind tibial spurs short but stout. Wings usually banded or patterned with brown, occasionally clear; vein R_4 occasionally with short appendix; cell Cu_2 frequently open. Hypopygium: 8th sternite relatively long and narrow; caudal ends of spermathecal ducts very slender, moderately chitinized.

Male

Eyes usually large and holoptic, occasionally narrowly separated in mid-line; upper facets usually, but not always, markedly enlarged. Palpi shorter than in ♀, of similar shape. Hypopygium undistinguished; style not as wide as in *Silvius*, tapering gently to a rounded point.

Distribution.—Cosmopolitan (about 260 species), but disappearing in the southern part of the southern hemisphere, and not known from the Pacific east of New Guinea and north Queensland (Part I of this series, Fig. 9).

There is a great range of variation in such characters as length of antennae, relative length of antennal segments, swelling of the 1st segment, development of shining facial calli, swelling of the fore tibiae, wing pattern, scutal ornamentation, and abdominal pattern, and various groups of species have been given subgeneric, or even generic, status. These are listed below.

Nemorius Rond.: Wings clear; face tomentose; 1st antennal segment not swollen.*

Turanochrysops Stack.: Wings clear; face with large, projecting, shining calli; 1st antennal segment swollen.

Liochrysops Philip: Wings clear; face entirely shining, bulging but without strong projections; frons also entirely shining, although callus clearly differentiated; 1st antennal segment not swollen.

Neochrysops Walt.: Wings evenly darkened; abdomen globose; antennae slender. Regarded as an abnormality by Bequaert (1930), but as a good genus by Philip (1947, 1954), who noted that a second specimen had been found.

Heterochrysops Kröb.: Wings with dark pattern; discal cell with a clear window. Not accepted as a natural group by later authors.

Kleineana End. (*Psylochrysops* Szil.): Wings with dark pattern; antennae very long and slender, at least as long as thorax including scutellum; fore tibiae more or less swollen; thorax often with tufts of golden hairs; slender species. Bequaert (1930) accepted this subgenus, but none of the characters is particularly reliable, and Oldroyd (1955) has rejected it.

Ziemannia End.: Wings with dark pattern; frons of ♀ extremely wide (Fig. 20*E*); face entirely tomentose; eyes of ♂ narrowly separated; 1st and 2nd antennal segments swollen. Bequaert (1930) treated *Ziemannia* as a synonym of *Chrysops* s.s., but it seems to be better distinguished than *Kleineana*.

Chrysops Meig.: Wings with dark pattern; antennae of moderate length, the 1st segment often swollen; fore tibiae rarely swollen; relatively thickset species.

I cannot comment on these, other than to say that the genus still seems to be radiating vigorously, and has probably not yet attained any degree of stability.

The early stages of about 40 species of *Chrysops* have been described (Hennig 1952). The eggs are usually laid in a single, overlapping layer on foliage overhanging water. The larvae are apparently always aquatic, Philip (1931) recording them from marshes, lakes, temporary ponds, running water, and later (Philip 1941*c*) from the margins of a salt lake, but not from more terrestrial situations. Most of the African material described by Neave (1915) was collected in the beds and banks of open and wooded streams. Actually, mature larvae and pupae have mostly been taken from soil or mud close to water, and the younger stages have rarely been seen. There is evidence that at least some species live on the bottom, where they feed on algae and debris in the mud. They are usually not predatory nor cannibalistic.

The larvae are fusiform in shape, and are distinguished by their small size, almost entirely striated body, unexpanded tracheal trunks, 2nd and 3rd antennal segments subequal or the 3rd longer than the 2nd, and nearly always by having a sharp, protrusible stigmatal spine. The pupae have the normal, 6-rayed aster, but lack both dorsolateral and lateral combs on the 8th abdominal segment; the antennal sheaths project beyond the edge of the head capsule, and the bristles on the frontal tubercles are double.

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* Dr. Philip has informed me that *Nemorius* is related to the *quadrivittatus* group of *Silvius*.

Genus SILVIOCHRYSOPS Szilàdy, 1922

Genotype: monotypic for *Silviochrysops flavescens* Szilàdy, 1922, Formosa.

I cannot place this genus, which seems to have a *Silvius*-like head, but a *Chrysops*-like wing pattern.

Distribution.—Formosa.

Tribe RHINOMYZINI Enderlein, 1922

Eyes bare; concolorous when relaxed in all species examined, except for different colour of upper, large facets of the males. Frons usually medium to wide (index 1.5 to 3.5), occasionally narrow, often flat and entirely shining; callus elongate, when differentiated from a shining frons. Subcallus and face often strongly projecting and shining, sometimes relatively flat and tomentose. Antennae short or long, modified in various ways, often biramous. Palpi often grossly inflated and shining, but sometimes quite simple and *Veprius*-like. Wings usually with extensive dark markings; vein *sc* setulose below; Cu_1 often with strong setulae above; R_4 without appendix; cells R_5 and M_3 open, Cu_2 occasionally open. Genitalia of ♀ often laterally compressed; undistinguished in ♂, except that the style often has a small subapical keel. Medium sized to large flies, generally of strikingly unusual appearance; exclusively Ethiopian and Oriental.

This group has radiated vigorously in tropical Africa (including the Malagasy subregion) in the same way that specialized Diachlorini have radiated in tropical America. The result in both cases is that some members of the tribe have come to differ more from one another than do the more conservative tribes from each other. If inflexible morphological standards were applied, it would be necessary to divide the group into three, perhaps four, tribes, and one would find major characters competing for recognition, as, for example, biramous antennae competing with laterally compressed ovipositor. It seems more reasonable and natural to accept the evidence of a burst of evolutionary activity, and to bring all the forms affected by it into a single tribal unit.

Doing so does not necessarily imply that the tribe is monophyletic, for an environment which stimulates one group may stimulate another, if it is capable of responding. However, the Rhinomyzini have structural features in common, which suggest that the tribe is at least predominantly monophyletic, and that it probably originated from the bouvieromyiine rather than the chrysopine stem.

Most of the species are inhabitants of dense rain-forest, in which many, if not all, breed in rot-holes in trees. Mr. Oldroyd (personal communication) has suggested that the unusual form of ovipositor, which is frequent in the tribe, may be an adaptation to this habit. Some species have been recorded as sucking blood, but the females of *Thaumastocera akwa* lack mandibles (Oldroyd 1954, Fig. 45), and Mr. Oldroyd has sent me a photograph, which demonstrates that they are also lacking in *Sphecodemyia lamborni.* It is unlikely that these species could pierce the skin of vertebrates, and Isaac (1925) did not observe *Gastroxides* to attack man or animals in India. It seems possible that blood-sucking may be confined to the less specialized members of the tribe.

Absence of mandibles in the female has been reported only in the two genera mentioned above and an aberrant tabanine, *Tabanotelum,* from Mauritius (Oldroyd 1954). Even more remarkable is the loss of the maxillae, although the mandibles are moderately developed, in the female of the Australian *Caenoprosopon trichocerus* (Pangoniini), which also is not known to suck blood. Reduction of mouth-parts under such conditions may not be as rare as one would have expected.

Ethiopian

Genus TABANOCELLA Bigot, 1856

Genotype: originally monotypic for *Silvius denticornis* Wiedemann, 1828, southern Africa.

Species examined.—denticornis (Wied.), ♂ ♀, det. Oldroyd.

Medium sized, parallel-sided, smooth flies, with biramous antennae and irregularly pictured wings.

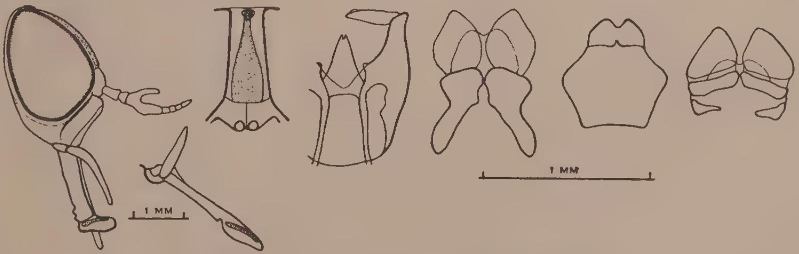

Fig. 21.—*Tabanocella denticornis* (Wied.).

Female

Frons medium (index 2.5), almost parallel, tomentose; callus pale, elongate-triangular, nearly full width of frons at base, and reaching anterior ocellus; ocellar tubercle small but prominent. Subcallus normal, lightly tomentose, with sparse hairs laterally. Face normal, tomentose. Antennae slender; 1st segment about one and a half times as long as wide; 2nd cup-shaped; 3rd with the basal section produced into a long dorsal prong, which reaches nearly to the base of the 4-annulate style. Palpi as long as shaft of proboscis, slender, tomentose, and with short, fine hairs. Proboscis normal; labella expanded and soft, but with small chitinous bars. Legs normal; hind tibial spurs well developed, slender. Wings with vein *sc* bare above, setulose below; Cu_1 with a complete row of setulae above. Hypopygium dorsoventrally compressed, without unusual features; notch between gonopophyses well developed.

Male

Eyes large, meeting on full length of frons; upper facets greatly enlarged, pale, contrasting strongly with a rather narrow zone of small blackish lower and posterior ones. Palpi shorter than in the ♀, narrowly torpedo-shaped, and markedly hairy. Wings with setulae on Cu_1 restricted to basal half. Hypopygium normal; style tapering to a point, and with a small subapical keel (Fig. 21).

Distribution.—About 11 species widely distributed in Africa (Gold Coast, northern Nigeria, Cameroons, Belgian Congo, Uganda, Kenya, Northern Rhodesia, Nyasaland, Tanganyika, Transvaal, and Zululand) and 10 from Madagascar (Oldroyd, personal communication).

Genus SPHECODEMYIA Austen, 1937

Genotype: *Sphecodemyia lamborni* Austen, 1937, Nyasaland, by original designation.

Species examined.—*lamborni* Aust., ♂ ♀, det. Oldroyd.

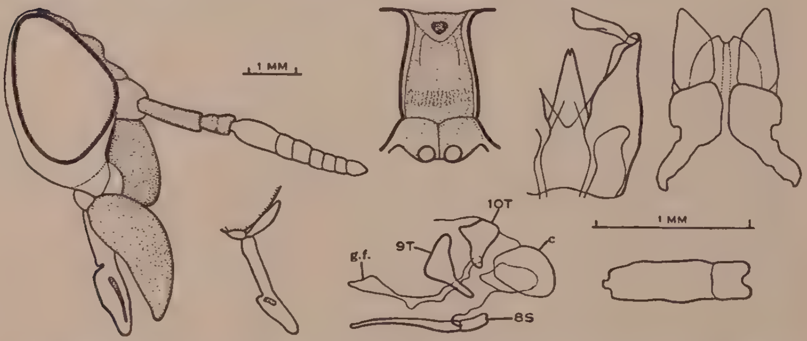

Fig. 22.—*Sphecodemyia lamborni* Aust. The terminal segments of the female are shown from the side, and the 8th sternite also from above. *9T*, 9th tergite; *10T*, 10th tergite; *8S*, 8th sternite and gonopophyses; *g.f.*, genital fork; *c*, cercus.

A remarkable, large, wasp-like form, with elongate antennae and a brown and yellow pattern on the wing.

Female

Frons wide (index 1.5), slightly diverging, longitudinally grooved, with a distinct bulge in the middle and a hollow above and below it, rather shining, and without clearly differentiated callus; vertexal triangle large and prominent, but ocelli small and placed close together (Fig. 22).

Subcallus strongly projecting, shining, but with irregular faint indications of tomentum, and with a few short but strong hairs on each side. Face strongly bulging, shining. Antennae as long as scutum; 1st segment cylindrical, about four times as long as wide; 2nd wider than 1st, and about half its length; both rather shining; 3rd *Chrysops*-like, about equal in length to 1st and 2nd together, tomentose, slightly swollen at base, and with 4 well-defined distal annuli, and 2-4 ill-defined annulations on the basal section. Palpi full length of proboscis, greatly swollen, tapering to a rounded point, shining, and covered with short hairs. Proboscis slender; labella with a lateral chitinous bar; mandibles absent. Legs long and strong; hind tibial spurs stout. Wings with vein *sc* bare above, setulose below; R_4 angulate, but without appendix; Cu_1 setulose above; cell Cu_2 sometimes just open at margin. Hypopygium laterally compressed; 8th tergite a pair of fused triangles; 8th sternite narrow and elongate, with a well-defined notch between the gonopophyses; 9th and 10th tergites lateral triangular plates.

Male

Eyes large, meeting in mid-line; upper facets markedly enlarged, reddish brown, contrasting with the blackish, smaller, lower facets. Face not as projecting as in ♀. Palpi much shorter than in ♀, not swollen, subcylindrical basally, and tapering gently to a point. Wings with vein Cu_1 bare above. Hypopygium: the two halves of the 9th tergite meeting for a considerable distance in mid-line; style swollen distally and without dorsal keel; at certain angles the distal end of the style appears almost globular.

Distribution.—Nyasaland (2 spp.).

Larvae of both species were found by Dr. Lamborn in rot-holes and forks of trees of the genera *Sterculia* and *Brachystegia*, always about 8-10 ft from the ground (Austen 1937). As many as a dozen might be found together, and they showed no indication of cannibalism, even when starved for 5 months in the laboratory. Lamborn thought that they fed on fragments of insects in the debris at the bottom of the holes. They did not mature until the rains set in. Austen gave a brief description of the pupa, which has large, ear-shaped prothoracic spiracles, conspicuous abdominal spiracles, and seems to be remarkable chiefly for the aster, which has a pair of very small dorsal rays, a large dorsolateral pair and a small ventral pair. It is noteworthy that an undescribed Australian species of *Cydistomyia* (Diachlorini), which breeds in rot-holes in *Casuarina* trees, has an aster of similar form.

Genus ORGIZOMYIA Grünberg, 1906

Genotype: monotypic for *Pangonia zigzag* Macquart, 1855, Madagascar.

Methoria Surcouf, 1909. Monotypic for *Pangonia zigzag* Macquart, 1855, Madagascar.

Species examined.—zigzag (Macq.), ♀, det. Philip.

A black, unusual looking species, with an irregular pattern of dark brown on the wings, and a superficial resemblance to the Australasian *Neobolbodimyia* (Tabaninae).

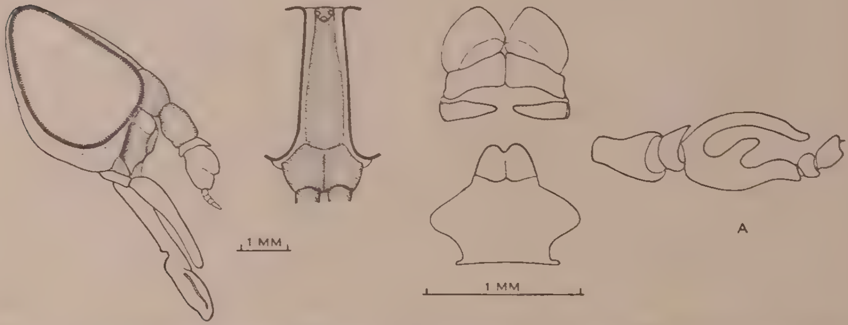

Fig. 23.—*Orgizomyia zigzag* (Macq.). *A*, antenna of female *Thaumastocera akwa* Grünb. (after Oldroyd 1954).

Female

Head flattened anteriorly, giving it an unusual triangular profile (Fig. 23). Frons medium (index 3.3), slightly diverging, with a narrow tomentose line along the eye, and all the rest raised and shiny, possibly representing a greatly enlarged callus; the ocellar tubercle is incorporated in the shiny area. Subcallus projecting in line with frons, shiny, and with strong black hairs on each side. Face not greatly produced, shiny, except for a patch of tomentum lateral to antennae; without hairs. Antennae: 1st segment relatively long and swollen, about twice as long as wide, shiny and hairy; 2nd wide but very short, cup-shaped, with a well-marked dorsal projection; 3rd with the basal plate wide and its dorsal angle carried forward to a projecting point, below which the plate is relatively thin, rather like a *Tabanocella* antenna with the space between the limbs filled in; style very small and short, 4-annulate. Palpi slender, spatulate, tomentose, longer than shaft of proboscis, which is as long as head height, rather slender, with large, soft labella strengthened by a pair of chitinous bars. Legs with tibiae somewhat swollen; hind tibial spurs long and strong. Wings with vein *sc* setulose above and below; Cu_1 setulose above. Hypopygium dorsoventrally compressed; 8th sternite rather strongly drawn out laterally, and gonopophyses unusually projecting.

Distribution.—Madagascar.

Genus THAUMASTOCERA Grünberg, 1906

Genotype: originally monotypic for *Thaumastocera akwa* Grünberg, 1906, Cameroons.

This remarkable genus has usually been placed in Tabaninae, because hind tibial spurs are completely lacking, but Ovazza and Taufflieb (1954) have shown that the caudal ends of the spermathecal ducts ("*manchons*") are simple, and Oldroyd (1954), on whose revision the following notes are largely based, has drawn attention to several points of similarity to members of the present tribe. There is no doubt that it is correctly placed here.

Robust, dark species, with dark wing pattern; not unlike *Orgizomyia*, but differing in several important particulars; illustrated by Surcouf (1921, Pl. 5, Fig. 11*a*) and Oldroyd (1954, Fig. 41).

Female

Eyes concolorous in life. Ocelli well developed. Frons narrow, nearly parallel, tomentose; callus oval at base, and with a parallel extension nearly to ocelli. Subcallus strongly projecting, shining. Face not strongly projecting, shining centrally, tomentose at sides; parafacials shining. Antennae short; 3rd segment (Fig. 23*A*), with long dorsal prong at base, and a 2nd one about middle of the basal plate of *T. akwa* ♀, though not in ♂ nor other species; style 2- or 3-annulate. Palpi considerably swollen in lateral view. Proboscis short; labella "small, and enclosed on each side by a chitinized plate, shaped like a mussel"; mandibles absent. *Hind tibial spurs absent.* Terminal segments of abdomen laterally compressed.

Male

Eyes meeting over considerable distance in mid-line; upper facets clearly marked off from the very small lower and posterior facets. Subcallus less prominent than in ♀. Palpi short and weak; 2nd segment club-shaped, barely half the length of the proboscis.

Distribution.—Guinean and Congo forest belts, from Sierra Leone to eastern Uganda (3 spp.).

Larvae were found by M. Collart in a rot-hole in the stump of a felled tree, in company with eristaline and other dipterous larvae on which they fed. The pupae have very small prothoracic spiracles, but large abdominal spiracles. Oldroyd (1954) suggested that the medium was probably deficient in oxygen and the pupae used the abdominal spiracles for respiration. The 8th abdominal segment is without combs, and the aster is peculiar, having no dorsal rays, a very large dorsolateral pair, almost dorsal in position, and a small ventral pair. Oldroyd thought that this form of aster might suggest relationship with Pangoniinae, but I would doubt it. Six-rayed asters occur in Pangoniini, Chrysopinae and Tabaninae, and probably represent the primitive condition in all subfamilies. The 2-rayed aster of Scionini would seem, therefore, to be a separate development from that of *Thaumastocera*, which may be in some way related to environment, for a trend in the same direction is seen in *Sphecodemyia* and the species of *Cydistomyia* mentioned above.

Genus THRIAMBEUTES Grünberg, 1906

Genotype: originally monotypic for *Thriambeutes singularis* Grünberg, 1906, Togo.

Guyona Surcouf, 1921. Monotypic for *Pangonia mesembrinoides* Surcouf, 1908, Tanganyika. Synonymy by Oldroyd (personal communication).

Hybommia Enderlein, 1922. Monotypic for *Hybommia nigripennis* Enderlein, 1925, Cameroons. Synonymy by Oldroyd, 1954. (Not a synonym of *Thaumastocera*, as thought by Bequaert, 1930).

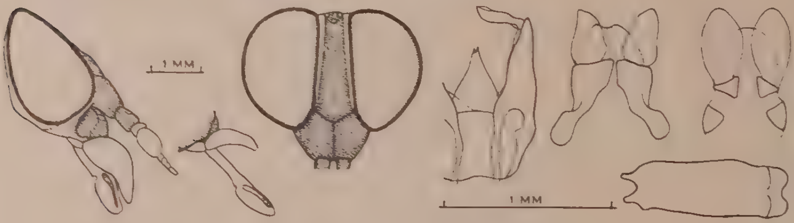

Fig. 24.—*Thriambeutes v-album* Surc.

Species examined.—*v-album* Surc., ♂ ♀, det. Oldroyd.

Generally rather like *Orgizomyia*, and with a similarly shaped head and frons, but differing in shape of antennae and palpi, wing markings, and laterally compressed ♀ terminalia.

Female

Subcallus even more projecting than in *Orgizomyia*; face strongly bulging forward; both highly polished and without hairs. Antennae with the basal section of the 3rd segment evenly rounded dorsally; style 4-annulate, longer than in *Orgizomyia*. Palpi greatly swollen, rounded above and tapering to a rounded point, soft and tomentose. Wings extensively darkened, with an oblique clearer band near middle; vein *sc* with a few setulae above, a strong row below; Cu_1 setulose on full length above. Hypopygium of *T. v-album* (Fig. 24) laterally compressed; 8th tergite a pair of triangles fused in the mid-line dorsally; 8th sternite long and narrow, with well-developed gonopophyses separated by a rather wide, shallow notch; 9th and 10th tergites divided into lateral triangular plates; remaining parts normal. Mr. Oldroyd has informed me that lateral compression is variable in this genus.

Male

Eyes large, meeting on full length of frons; upper facets greatly enlarged, pale, contrasting strongly with the dark lower ones. Face not as produced as in ♀. Palpi similar to ♀, but shorter and not so swollen. Wings as in ♀, but *sc* entirely bare above. Hypopygium normal; style with a similar keel to *Tabanocella*.

Distribution.—Five species from Togo, southern Nigeria, Spanish Guinea, Belgian Congo, Nyasaland, Tanganyika, Mozambique, and Bechuanaland.

Bequaert (1930) was inclined to regard *Thriambeutes* as congeneric with *Orgizomyia,* which has page priority, but the differences between them are considerable, and I believe that they should be maintained as distinct. Austen (1937) noted that Lamborn had found the larvae of *T. v-album* in rot-holes and forks of trees, similar to those from which the two species of *Sphecodemyia* were obtained.

Genus HINEA Adams, 1905

Genotype: originally monotypic for *Hinea flavipes* Adams, 1905 (= *Silvius pertusus* Loew, 1858), southern Africa.

Close to *Thriambeutes,* from which it apparently differs essentially in having a biramous 3rd antennal segment, like that of *Tabanocella.* The general habitus, tapering abdomen, probably compressed "ovipositor", and basic wing pattern are similar in the two genera, and both have been found to breed in rot-holes in trees. It is possible that subgeneric separation might be more appropriate, in which case *Hinea* would have priority.

Distribution.—About eight species from French Congo, Belgian Congo, Northern Rhodesia, Nyasaland, Southern Rhodesia, Transvaal, Bechuanaland, and South Africa.

Dr. Lamborn found the larvae of *H. bicolor* Aust. in rot-holes of *Brachystegia* sp. at 2500 ft above sea-level. They differed from the larvae of *Sphecodemyia* in being cannibalistic, and the pupae also differed in having the spines of the abdominal circlets shorter, stouter, more rigid and less numerous, and the lateral arms of the aster much larger (Austen 1937).

Oriental

Genus GASTROXIDES Saunders, 1841

Genotype: originally monotypic for *Gastroxides ater* Saunders, 1841, India.

Ditylomyia Bigot, 1859. Monotypic for *Ditylomyia ornata* Bigot, 1859, Ceylon. Synonymy by Ricardo, 1911.

Species examined.—ater Saund., ♂ ♀, det. Philip.

A black species, with heavily patterned wings, tapering abdomen, and a general resemblance to *Thriambeutes,* but with more rounded eyes, wider frons, and longer, biramous 3rd antennal segment.

Female

Frons wide (index 2), diverging, somewhat tomentose at sides, but mostly shining, and with a raised mass above subcallus and another just below middle; ocellar tubercle raised, prominent, shining. Subcallus projecting, dark, but not shining, and with strong dark hairs laterally. Face strongly bulging forward, shining. Antennae nearly as long as scutum; 1st segment cylindrical, shining, about three times as long as wide; 2nd similar, but about half as long as 1st, and with an incipient annulation at middle; 3rd a little longer than 1st and 2nd together; basal section with a strong dorsal prolongation, beyond which is an incipient annulation; style wide, continuous with basal section, 4-annulate. Palpi as long as proboscis, distinctly swollen, though not as much as in *Thriambeutes,* tapering to a blunt point, somewhat shiny, and with short dark hairs. Proboscis normal; labella with chitinous bars. Wings with vein *sc* setulose above and below; Cu_1 irregularly setulose above; cell Cu_2 just open at margin. Hypopygium strongly laterally compressed, essentially similar to *Thriambeutes* and *Sphecodemyia.*

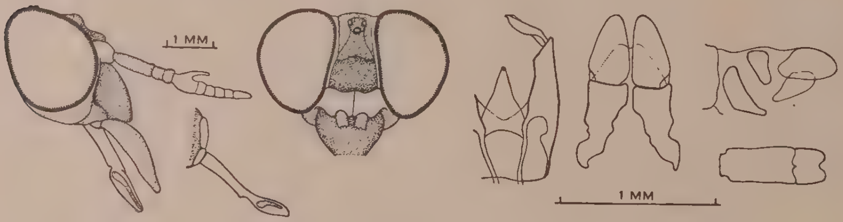

Fig. 25.—*Gastroxides ater* Saund.

Male

Differs from ♀ in having orange 2nd abdominal tergite. Eyes meeting in mid-line on full length of frons; upper facets markedly enlarged, sharply differentiated from the small, darker lower facets. Subcallus small and rather dull. Face shining, but not as bulging as in ♀. Antennae more slender than in ♀, and the dorsal prong on the 3rd segment quite short. Palpi shorter than in ♀; 2nd segment subcylindrical, rounded apically, and with a small bare area near tip. Hypopygium similar to related genera; style with a small keel.

Distribution.—Six species from central and eastern India, Ceylon, Malaya, Java (Schuurmans Stekhoven 1926, 1928), and east China (Ôuchi 1939).

Though differing somewhat in eyes and frons, there are so many resemblances in other respects, that there is no room to doubt that *Gastroxides* developed from the same stock as the African members of the tribe, and it also breeds in rot-holes in trees (Isaac 1925). His figure of the pupal aster (which may have the ventral side up) shows the lateral rays to be the biggest, but the dorsal and ventral not as reduced as described for *Sphecodemyia* and *Thaumastocera.*

Genus RHINOMYZA Wiedemann, 1820

Genotype: monotypic for *Rhinomyza fusca* Wiedemann, 1820, Java.

This species long remained unrecognized. The original description certainly suggests an insect like *Gastroxides,* and Bequaert (1930) expressed the opinion that the two were probably congeneric. Mr. Oldroyd, however, has informed me that he has recently seen a male which agrees with Wiedemann's description, and he is inclined to doubt the identity of the two genera. Redescription of the genotype is important, as it is also the type of the tribe.

Distribution.—Java.

ACKNOWLEDGMENTS

I have been particularly helped in the preparation of the present Part of the series by a long correspondence with Mr. H. Oldroyd about the subgenera of *Mesomyia*, as a result of which my treatment of this group is, I believe, much better balanced than it could otherwise have been. My indebtedness to him and my other colleagues for named material and information about other genera will be apparent from the text.

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ADDENDUM

Material received since this paper went to press has made it possible to expand two of the definitions.

Subfamily **SCEPSIDINAE**

Genus BRAUNSIOMYIA

Species examined: *cinerea* (Surc.), ♂ ♀, det. Oldroyd.

Female

Eyes with sparse, fine hairs, which are just visible at ×15; inner margins sharply angulate at top of subcallus. Frons extremely wide (index less than 0.5), converging; ocellar tubercle flat; callus (Fig. 26) very wide, shining; a shining black spot also at vertex on either side of ocellar triangle. Subcallus tomentose, without hairs. Parafacials wide; face convex; tentorial pits deep and prominent. Antennae with third segment 7-annulate, the terminal annulus small, and the subdivisions between the annuli better defined than in *Adersia*. Palpi with first segment slender; second globular, its apical pit relatively shallow. Proboscis with clearly developed labella. Hind tibial spurs long and slender. Wing with vein *sc* setulose below, bare above; R_4 angulate and with rudimentary appendix; M_1 and M_2 abbreviated, not reaching wing margin. Hypopygium generally similar to that of *Scepsis*; 8th sternite strongly arched laterally, with shallow notch between gonopophyses; 9th tergite a large plate, the central hairy portion differentiated from the smooth, lightly chitinized marginal area; 10th tergite triangular, membranous, cerci long, prominent, and provided with a series of strong, spatulate spines, not unlike those of Asilidae; caudal ends of spermathecal ducts long, lightly chitinized, with a distinct annular thickening; remainder of ducts unusually short, as in *Adersia,* but without globular swelling; spermathacae (Fig. 26) of unusual shape.

Male

More hairy than female; eyes larger, not so widely separated. Frons converging, index less than 1, tomentose and hairy; ocellar tubercle convex, but not as prominent as in *Adersia*; a short, narrow callus extending down from median ocellus, as in *Adersia,* but, in addition, an oblique shining patch on each side above subcallus. Face more sunken than in female, but apical pits of palpi deeper. Hypopygium: 9th tergite an arched shield, as in Pangoniinae, with only a median line to indicate possible incipient subdivision; style simple, scionine-like, bluntly rounded at tip; aedeagus smooth, unusually long; flagella large; median muscle strut with racquet-shaped expansion and strong dorsal keel, somewhat like that of *Mycteromyia* (Part II, Fig. 23).

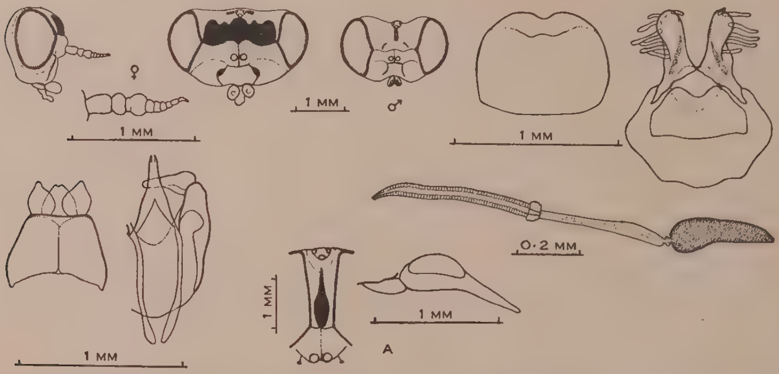

Fig. 26.—*Braunsiomyia cinerea* (Surc.). One complete spermathecal duct and spermatheca shown at right. *A,* frons and palp of *Mesomyia* (*Pareucompsa*) *femoralis* (Ric.), ♀.

This remarkable insect provides additional evidence to justify maintaining the group as a separate subfamily between the Pangoniinae and Chrysopinae. The antennae and male genitalia are pangoniine; the callus and setulae on *sc* are chrysopine; and the female genitalia ally it with *Scepsis.* Thus, we now have *Scepsis,* which is pangoniine in all recorded features except proboscis, palpi and female genitalia, *Adersia,* which leads towards Chrysopinae in genitalia of both sexes, and *Braunsiomyia,* which leads towards Chrysopinae in frontal callus and setulae on *sc.* There are still so many points of resemblance between the three genera that the group cannot on present evidence be regarded as polyphyletic, but its definition must be amended to include the new findings.

Subfamily **CHRYSOPINAE**

Subgenus PAREUCOMPSA

Species examined.—femoralis (Ric.), ♀, det. Oldroyd.

Female

Eyes bare; blue-black, with a wide, oblique blue band narrowly bordered with green (relaxed). Frons converging; callus Indian club-shaped. Subcallus tomentose, without hairs. Face rather elongate, tomentose, with very short, inconspicuous hairs. First antennal segment not enlarged nor hood-like dorsally; third missing. Palpi with an unusual, swollen bare area on basal half (Fig. 26*A*). Labella with a narrow chitinous bar. Hind tibial spurs short and stout. Wing with vein *sc* bare above and below. Genitalia as in subgenus *Pseudotabanus*.

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A REVIEW OF AUSTRALIAN SCENOPINIDAE (DIPTERA)

By S. J. Paramonov*

(*Manuscript received May 11, 1955*)

Summary

A preliminary attempt is made to review the Australian Scenopinidae. The Australian fauna consists of five genera, having about 12 species (two new genera, *Scenopinula* and *Riekiella*, are described and the genus *Pseudomphrale*, with two new species is recorded here for the first time from Australia). Morphology, bionomics, and geographical distribution are also discussed.

I. Introduction

This paper is a preliminary attempt to review the Australian Scenopinidae. Only two genera were previously recognized, *Scenopinus* (Meig.) and *Pseudatrichia* Osten-Sacken, with a total of 3-4 species. The discovery of two new genera (*Scenopinula*, gen. nov., and *Riekiella*, gen. nov.), and the record of the genus *Pseudomphrale* Kröber (with two new species), show that the Australian fauna is much richer than previously thought. It is to be expected that in future more genera and species will be found, for the study has only started, and not all the Australian collections were examined for this paper.

The family Scenopinidae or "window flies", is represented very poorly in all Australian museums, few possessing more than about six specimens. They are not abundant in nature, but are not as scarce as would appear from their representation in museums. Their small size and rare presence on flowers possibly explain their scarcity in collections. However, if one gives enough attention to these flies, numbers can be collected, especially on windows. The larvae of scenopinids are of economic importance in killing the larvae of moths in carpets, etc.; more study and intensive collecting would be of interest to the practical, as well as to the theoretical entomologist.

Because so few members of the Australian fauna are known, students of this group should be familiar with the major works by overseas authors, otherwise they will find it difficult to determine the true relationships of Australian species to the world fauna. The most important works the author has consulted are those of Lundbeck (1908), Verrall (1909), Kröber (1914), Brunetti (1920), Séguy (1926), Curran (1934), and Lindner (1949).

II. Bionomics

Adult

The adults, with the exception of *Scenopinus fenestralis* (L.) are not common in collections. The flies are not very common, but sometimes occur

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on windows, especially in stables and out-buildings, where they can be collected much more easily than in the field. They are xerophiles and are poor fliers. The common name of the family is derived from the window-frequenting habit.

Larva

Bouché (Naturgesch. d. Ins., 1834, 46, Tab. iv, Figs. 21-25) describes larvae and pupae of *fenestralis* (*senilis*); the larvae were found in polypori, on *Salix*, and other trees. Léon Dufour described the pupa of *fenestralis* (Ann. Soc. Ent. Fr., ii.8.1849, p. 493, Plate 16, Fig. iv). Frauenfeld (Verh. zool.-bot. Ges. Wien, xiv, 1864, p. 65) bred *fenestralis* from larvae found among horse hair in a mattress. He considered (p. 68), probably correctly, that three larvae from the nest of a swallow which Loew (Verh. zool.-bot. Ges. Wien, xi, 1861, p. 395) had recorded as *Thereva* larvae were larvae of *Scenopinus*. *S. niger* was bred by Damianitch (Verh. zool.-bot. Ges. Wien, xv, 1865, p. 237) from a pupa found in an elm tree in a cocoon of *Saturnia pyri* which contained the remains of the *Saturnia* pupa. Jaennicke (Berl. Ent. Z., 1867, p. 78) mentions the same species bred from larvae in decaying wood. Packard (Proc. Essex Inst., 1867, p. 93) mentions and figures a *Scenopinus* larva which was stated to have been feeding on carpets. Perris (Ins. du pin marit. Ann. Soc. Ent. Fr., 1870, p. 226) found larvae and pupae of *S. fenestralis* in a branch of *Crataegus* which contained larvae of *Ptinus germanus*, and in pine-boards with larvae of *Hylotrupes bajulus*; he also observed a *Scenopinus* larva devouring a pupa of *Hylotrupes*, and also mentions a pupa of *Lucilia dispar* found in a swallow's nest containing a *Scenopinus*. Waterhouse (Proc. R. Ent. Soc. Lond., 1881; Ent. Mon. Mag., 1882) bred *S. fenestralis* from larvae from the root of *Aconitum*. Hagen (Canad. Ent., xviii, 1886, p. 129) mentions the larva of *S. fenestralis* (*pallipes*) found under a carpet near the empty case of a *Tinea*.

The larva closely resembles that of a *Thereva*. It is elongated, cylindrical, hard to the touch, and apparently consisting of 20 segments; the head is small, brown; at the apex of the body there are 2 small styles. The larva moves with serpent-like movements. The pupa also resembles that of *Thereva*, being somewhat slender, and having on the front of the head the antennal sheaths in the form of 2 spines directed to each side. The abdominal segments have girdles of spines and bristles, and along the sides of each segment there is a protuberance with bristles; the apex terminates in 2 conical projections each with a bristle.

The larvae are certainly carnivorous. According to the evidence recorded above, the larva of *S. fenestralis* seems to live in houses, probably feeding on the larvae of moths, on psocids, and the like. This is consistent with the common occurrence of *fenestralis* on windows; but according to Bouché the larva may also live in the open as he found them in tree-fungi. This also is not improbable, as the larva could have been feeding on other larvae present there. A record by Assmus (Stettin. Ent. Ztg., 1863, p. 401) that he had found the larva of *fenestralis* in overripe strawberries is most probably an error as he describes the pupa as being enclosed in a light cocoon. The larva of *niger* seems to live in the open. According to the records the larva seems to hibernate, the development of pupa and imago taking place in spring.

III. GEOGRAPHICAL DISTRIBUTION

The family is distributed in all regions of the world, and about 60 species are known.

IV. SYSTEMATIC POSITION OF THE FAMILY

The Scenopinidae is a very limited, but distinct family, whose systematic position is doubtful. Its characters indicate diverse affinities, such as to *Xylomyia*, the Therevidae, and Mydaidae. Verrall places them with the latter in a superfamily Dermatinae, between the Asilidae and Therevidae. Lundbeck and Kertész put them between the Therevidae and the Empidae; Schiner with Mydaidae between Asilidae and Therevidae; Aldrich between Therevidae and Bombyliidae; in 1914 Kröber put them with Nemestrinidae, Cyrtidae, and Bombyliidae in the group Tromoptera, with closest relationship to Therevidae; Séguy in 1951 placed this family near Therevidae and Apioceridae.

V. SYSTEMATICS

Family **SCENOPINIDAE**
(window flies)

Adult

Small, elongate, nearly bare flies, usually from 2 to 7 mm long, mostly of a dark colour (Fig. 1); entire body free of bristles; head, thorax, and abdomen of nearly equal width; antennae and proboscis very short.

Head nearly semicircular, flattened in front and almost straight behind, not quite close to the thorax. Frons and face nearly flush with eyes, or so slightly sunk that the eyes cannot be termed bulging; face broad, but very short and quite bare; epistoma short, retreating. Proboscis very short, withdrawn, labella broad. Palpi cylindrical or slightly clavate, with sparse bristles at the tip. Frons flat or slightly sunken, or (rarely) very swollen, surface smooth or wrinkled. Eyes bare, usually (but not always) touching in the male, and separated in the female by the wide frons; when the eyes touch, the facets on the upper half and more are enlarged; in life they bear coloured bands. Antennae inserted below middle of frons, close together at base, comparatively very short; 3-jointed, basal joints short, 3rd joint elongated, strap-shaped, bent downwards, and without any distinct style or arista, but with some excavation on underside.

Thorax oblong, being rather longer than broad, dorsally rather flattened and yet appearing humpbacked because the head is depressed; absolutely without bristles, but with very short scaly pubescence on the disc, and with minute pubescence on the pleura; metapleura without any tufts of hairs. Scutellum broad, short, flat, and unarmed; metanotum rather large but not conspicuous.

Wings when at rest, lying flat along the body, covering the depressed abdomen. Membrane of wing microscopically pubescent, without small wrinkles, sometimes (*Lepidomphrale*) with scales. Veins few and simple. Costal vein ending well before the wing tip; at apex of subcostalis usually not straight, but basad as a hump; ambient vein absent. Third longitudinal vein branched, fork commencing nearly level with end of discal cell. Vein r_1 and r_{2+3} running parallel and extremely close to one another. First posterior cell (usually) open or long petiolated. Basal cells long, the upper basal cell (R) much longer than the lower one (M). Vein m_1 always running into the costa, or at least in the apex of wing, never in the hind margin of wing. Anal cell large, long petiolate, at apex acute.

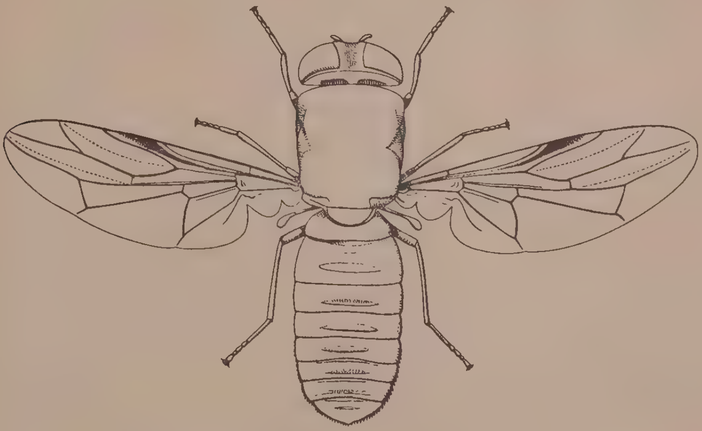

Fig. 1.—*Scenopinus fenestralis* (L.). Adult.

The position of cross vein *r-m* is changeable and plays a role in the identification of species; also the length, shape, and position of the vein r_4 in comparison with r_5 play an important role. There are only 3 posterior cells.

Alula small. Squamae alares small, but fairly well developed and bearing very short fringes; thoracic squamae almost absent. Halteres in no way concealed, knob large.

Legs usually short, stout (in *Pseudatrichia* long and thin), and entirely unarmed; tibiae never spurred, though some small bristles may have a spur-like appearance. Pulvilli, 2, small but distinct, empodium a thin bristle only.

Abdomen flattened, with 7 or 8 segments, each segment bearing an impressed transverse channel across its middle; the membranes between some of the segments usually bearing narrow white bands in the male. Genitalia of the male rather knobbed; ovipositor concealed.

Larva

Body worm-like, very long, hard, smooth, elastic, with 20 segments plus head. Head elongated, pointed, strongly chitinized, yellow (Fig. 2). Antennae very small, filiform. Palpi biarticulate, 2 pairs of sensorial bristles; mandibles strong, pointed, curved, moving vertically. There is a chitinized and articulated prolongation at base of the head, extending inside and above the whole prothoracic segment, the last segment working as a pseudopode.

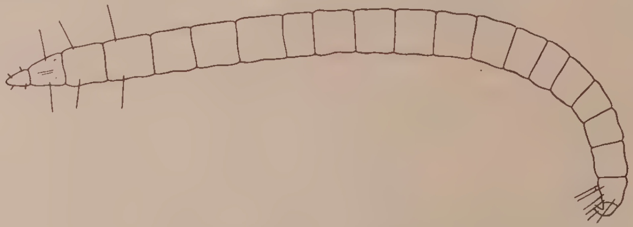

Fig. 2.—*Scenopinus fenestralis* (L.). Larva.

KEY TO GENERA OF THE FAMILY SCENOPINIDAE

1. First posterior cell closed, with a long petiole 2
   First posterior cell open or the vein m_1 not reaching the hind margin of wing 3
2. First submarginal cell much broader than the discal cell. Body and legs very elongate. Horizontal diameter of head distinctly greater than vertical .... *Pseudatrichia* O-S.
   First submarginal cell nearly as broad as the discal cell. Body and legs of usual proportions, not very elongate. Vertical diameter of head greater than horizontal ....*Pseudomphrale* Kröb.
3. Frons very swollen, tuberculate. Veins r_5 and m_1 quite parallel; the vein r_4 is slightly longer than cross vein *r-m* ....*Scenopinula*, gen. nov.
   Frons normal, not tuberculate. Veins r_5 and m_1 distinctly converging towards the hind margin of wing; vein r_4 is much longer than cross vein *r-m* 4
4. Third antennal joint with 2 acute apices. Vein m_1 not reaching the hind margin of wing. Eighth segment of abdomen (♀) as long as 2 preceding segments combined, elongate, conical ....*Riekiella*, gen. nov.
   Third antennal joint rounded at apex, never with acute prolongation. Vein m_1 always complete. The last segment is, at most, as long as the preceding one ....*Scenopinus* (Meig.)

Genus PSEUDATRICHIA Osten-Sacken

Pseudatrichia Osten-Sacken, 1877, Bull. U.S. Geol. Surv. 3: 276.

Body extremely elongate, slender, with slightly metallic shine. Head almost spherical. Eyes in male narrowly separated. Antennae shorter than head, deeply sunken. Abdomen about 2.5 times as long as thorax. Legs very long and slender. Wings very long. First posterior cell closed, with a long petiole. About six species are distributed in North America.

Only *P. mariaensis* Hardy is known from Australia at the present time.

PSEUDATRICHIA MARIAENSIS Hardy

Pseudatrichia mariaensis Hardy, 1933, Proc. Linn. Soc. N.S.W. 58: 419, text-fig. 3.

The description given by Hardy is as follows:

"♀. Head as wide as or slightly wider than thorax; elongate, so that seen laterally it is somewhat elliptical. Frons wide, one-quarter the width of the head at its narrowest part. The head behind the eyes is very bulging, no flange is formed and so the cavity behind the eyes is slight. Seen laterally the ocellar tubercle stands above the eyes and the frons is mainly hidden. The frons is shining, but there are two rows of punctures each side of the median depression; these punctures stop before reaching the ocellar tubercle. In conformity with the elongate head, the face recedes abruptly. The hairs of the head are more abundant than those of the preceding species (*S. civiculus*) and somewhat yellowish. The antennae have the third segment only two and a half times the length of the first and second segments combined, rather conical in shape and with a small depression at the apex.

The thorax is black, rather densely covered with punctures and yellow hairs. The semicircular scutellum is scarcely punctured, shining and bulging, being divided from the thorax by a deep depression. The posthumeral callus has a strong tendency towards being brown. The black abdomen is conspicuously wrinkled, considerably longer than the head and thorax united, and widest at nearly half its length. It has a vestiture of rather long, black, moderately abundant hairs towards the apex. The legs are black, the wings hyaline, with brown veins. The halteres are black.

♂. Agrees with the female in general shape and colour, except that the abdomen is metallic blue-black with white edges at apex of segments. The frons is reduced in the centre so that the eyes are nearly approximate there. The post orbital margins are prominent.

Length of both sexes, 5 mm.

Hab.—Tasmania: Maria Island, 29th December, 1915, 1 ♂, 1 ♀, in perfect condition, taken *in copula*, probably by sweeping along the shore or close to it."

The author has studied one specimen, ♂, 15.i.1952, Mt. Lofty, 2334 ft, S. Australia (Miss H. M. Cane), and can add the following details: Head extremely long, its horizontal diameter 1.5 times as long as vertical diameter, flattened from above. Frons with a very characteristic structure, hour-glass-like; the occipital part occupied by ocellar triangle and the space before the anterior ocellus; at narrowest point frons as broad as anterior ocellus, antennal half of frons shining, polished, with microscopic yellowish hairs. Discal cell extremely narrow, even at apex, narrower than the 1st basal cell; cross vein *r-m* at the middle of discal cell. The extremely narrow and long body, which is at least twice as long as thorax, and the long, very slender legs are characters more typical of this genus than the closed 1st posterior cell. Lack of material prevented further study of this very interesting group.

Genus PSEUDOMPHRALE Kröber

Pseudomphrale Kröber, 1913, Ann. Hist. Nat. Mus. Hung. 11: 180.

This genus was known only from the Palaearctic Region (Central Asia). It differs from typical *Scenopinus* mainly in the closed and long petiolated first posterior cell.

Eyes in male quite contiguous. Third antennal joint extremely short. Mesonotum with distinct white pattern. Abdomen with white cross bands.

KEY TO AUSTRALIAN SPECIES OF THE GENUS PSEUDOMPHRALE

1. Base of vein r_4 situated nearly at end of 1st third of 1st posterior cell. Anterior part of mesonotum with small whitish scales. Length of body 5 mm ....*P. waterhousei*, sp. nov. ♂
   Base of vein r_4 is situated nearly at the middle of 1st posterior cell. Mesonotum only haired. Length of body 2 mm ....*P. westralica*, sp. nov. ♂

PSEUDOMPHRALE WATERHOUSEI, sp. nov. ♂

Whole vertex occupied with a big, equilateral, ocellar triangle, eyes nearly touching below anterior ocellus, but with a very fine, hairless, stripe separating them, lower frons diverging narrow, covered rather densely with short, yellowish hairs. Postocularia (occipital part behind eyes) nearly absent, a high coronet quite absent. Antennae rather long, nearly as long as haired part of frons. Both basal joints of antennae together equal to about one-third of 3rd antennal joint, which is very elongate, egg-shaped. All facets of a nearly-equal size. Face at level of proboscis occupying about one-third of head width. Palpi comparatively very long, narrow, nearly reaching apex of mouth cavity, proboscis distinctly longer than palpi.

Mesonotum anteriorly and laterally covered with microscopic scales, which are triangular or nearly egg-shaped (very similar to those in the genus *Agapophytus* (Therevidae)); similar scales on mesopleura and at sides of 2nd and 3rd tergites as well as at sides of some sternites, but not so dense. Hind part of mesonotum also with usual, microscopic, yellowish hairs. Legs dark, tibiae and tarsi slightly paler. Halteres dark.

Wings hyaline, with yellow veins. First posterior cell long, petiolate, the last portion of r_5 about as long as vein closing discal cell.

Anal cell long, closed very far from hind margin; the distance is about as long as that between vein *r-m* and the one closing the discal cell. Vein r_4 very long, running nearly parallel to vein r_5, separating at a very acute angle; point of separation situated nearly at same level as apex of r_{2+3} and that of discal cell. Cross vein *r-m* distinctly beyond middle of discal cell.

Abdomen short and broad, black, bare; nearly whole surface of 6th-8th tergites ivory, with some dark triangular spots at sides; genitalia dark. Underside, at sides, with yellowish microscopic scales and with some hairs medially.

Length of body 5 mm, of wing 3.5 mm.

1 ♂ (type), 20.i.1935, Killara, New South Wales (D. F. Waterhouse).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

It is evident that this species does not belong to the genus *Pseudatrichia,* because only the possession of one formal character (closed 1st posterior cell) justifies its inclusion in that genus.

PSEUDOMPHRALE WESTRALICA, sp. nov. ♂

Easily distinguished from *Pseudatrichia mariaensis* by broad thorax and abdomen, being a typical *Scenopinus*; it differs from *P. waterhousei* in the uniformly coloured abdomen.

Eyes touching on a line for a distance a little longer than the remainder of frons. Frons extremely small, sunken, in upper part whitish, quite bare. Postocular part undeveloped. The upper half of eyes with enlarged facets. Mouth cavity very deep below the antennae. Proboscis very short. Antennae extremely short, nearly as long as one-fourth of longitudinal diameter of eye; tip of antenna bifurcated. Third antennal joint of an unusual pear-like form. Underside of head with whitish, microscopic hairs.

Thorax, as whole body, dark brown, mesonotum black, humeral and postalar calli yellow. Wings hyaline; venation normal; the portion of the vein m_1 beyond cross vein $r\text{-}m$ short, only slightly longer than the vein closing the discal cell. Halteres yellow. Legs brown.

Abdomen uniformly brown. Genitalia rather large and broad, with some whitish hairs.

Length of body 2 mm, of wing about 2 mm.

1 ♂ (type), 21.viii.1926, Zanthus, W. Australia.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Genus SCENOPINUS (Meigen)

Omphrale Meigen, 1800, Nouvelle classif. 29: 52.
Scenopinus Latreille, 1802, Hist. Nat. Crust. Ins. 3: 463; 1804, 14: 392.
Atrichia Schrank, 1803, Fauna Boica 3: 54.
Cana Schellenberg, 1803, Gattung der Fliegen, p. 66.
Hypselura Meigen, 1803, Illiger's Mag. 2: 273.
Astoma Lioy, 1864 (nec Oken 1815), Atti Ist. Veneto (3), 9: 762.

Generotype *Musca fenestralis* L. by Latreille's designation.

Species of rather small size, very slightly hairy, and of black or blackish colour; in the male generally with white incisures between some of the abdominal segments. Head as broad as thorax and broader than high, arched in front, slightly excavated behind. Eyes either touching in the male and well separated in the female, or separated in both sexes and with only a slight difference in the breadth of the frons according to the sex; the eye facets in the male are, in the first case, larger above than below with a distinct dividing line; in the second case they are of equal size. Antennae inserted near to each other, below the middle. Jowls not descending below the eyes, very small, forming only a narrow rim. Antennae 3-jointed, the 1st 2 joints small, the 3rd large. Epistoma very short and retreating. There is no oral cone; clypeus somewhat horseshoe-shaped, stretching horizontally from the epistoma to the labrum. Proboscis short; labrum triangular, truncate, short, as long as the basal part of labium; maxilla with a pointed lacinia, slightly longer than the labium, and with 1-jointed, slightly club-shaped palpi which are rather long, longer than the lacinia; hypopharynx weak; labium with a short basal part and rather large and broad labella about twice as long as the basal part; at rest the proboscis is quite withdrawn. Thorax rectangular, considerably longer than broad; no macrochaetae present. Abdomen somewhat long, flattened above, with nearly parallel sides, as broad as thorax; it consists of 7 visible, not transformed segments, the 2nd being the longest; the segments have transverse impressions on the dorsal side. The genitalia consist in the male of 2 broad lamellae above and a considerably arched plate below which is cleft in the hind margin; the female genitalia consist of an 8th, normally developed segment, and a small terminal part. Legs somewhat strong, without bristles, but with small apical spurs on the tibiae; sometimes the hind tibiae are thickened. Claws small, with 2 pulvilli but no empodium. Wings with the cubital vein branched and thus with 2 cubital cells; the discal vein not branched, the apical part curved up towards the end of the cubital vein; thus the 1st posterior cell narrows at the margin; as the discal vein is not branched there is no real discal cell, but this is formed below in its whole length by the upper branch of the postical vein; the discal cell is long; the 1st basal cell longer than the 2nd; the anal cell is closed at a considerable distance from the margin. Alula developed; alar squamula slightly fringed at the margin, no thoracic squamula, but frenulum distinct. When at rest the wings lie parallel over the abdomen, one quite covering the other, and they are also inclined somewhat downwards at the sides, the fly thereby having a curious appearance.

KEY TO AUSTRALIAN SPECIES OF THE GENUS SCENOPINUS*

1. Males 2
   Females 6
2. Eyes distinctly separated 3
   Eyes contiguous .... *S. fenestralis* (L.), ♂
3. Eyes at vertex occupying nearly one-fifth of the head width. Facets of equal size. Hind tibiae slightly swollen .... *S. nigra* De Geer, ♂
   Eyes separated below the ocelli by a very narrow, linear stripe. Facets in upper two-thirds distinctly larger than in the lower third. Hind tibiae not swollen ... 4

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* Some European species, which have probably been introduced into Australia, but have not previously been recorded, are also included.

4. Legs pale yellow. Antennae reddish yellow. Halteres yellow. Frons shining, as if polished .... *S. glabrifrons* Meig., ♂
Legs brown or blackish, at most the tibiae and tarsi yellowish (the male of *S. papuana* unknown). Another complex of characters 5
5. Discal cell distinctly broadened at apex. Femora and tibiae black .... *S. perkinsi* Hardy, ♂
Discal cell nearly parallel-sided. Femora dark, tibiae reddish yellow .... *S. biroi* Kert., ♂
6. Frontal stripe below anterior ocellus about as broad as ocellar triangle. Postocular flange absent .... *S. perkinsi* Hardy, ♀
Frontal stripe always broader than ocellar triangle 7
7. Posterior edge of eyes with a moderately broad or broad margin (flange) 8
Posterior edge of eyes with, at most, only very fine linear margin 10
8. Legs black. Wings strongly suffused with brown. Knob of halteres blackish or brown .... *S. nigra* De Geer, ♀
Legs reddish yellow or yellowish brown, never black. Wings hyaline. Knob of halteres nearly whitish 9
9. Frons shining, polished .... *S. glabrifrons* Meig., ♀
Frons dull, not shining .... *S. fenestralis* (L.), ♀
10. Length of body 2.5-3.5 mm. Legs yellow. Discal cell nearly parallel-sided. Frons about ¼ of head width .... *S. biroi* Kert., ♀
Length of body 4-4.5 mm. Legs, at least femora, dark brown. Discal cell distinctly broadened at apex. Frons narrow, at most one-fifth of head width .... *S. papuana* (Kröb.), ♀

SCENOPINUS FENESTRALIS Linné ♂, ♀

Omphrale fenestralis Linné, 1845, Fauna Suec. (Musca) (1761).
Scenopinus fenestralis Verrall, 1909, British Flies 5: 597.

Verrall writes: "♂. Dull black, very densely and coarsely punctate, almost shagreened. Face scarcely existing because the large mouth-opening occupies almost all the space below the antennae, but the narrow bare side-cheeks are dark greyish and slope down into the epistomal depression, which has its upper boundary distinctly above the antennae so that the antennae arise from within it; the eyes rapidly diverge from the top of the frons down to their lowest part where their interval is about twice as wide as at the antennae; at the back of the mouth-opening is some thin grey pubescence, which extends along the narrow jowls and part way up the shallow back of the head, but dies away about half-way up; upon close examination a narrow bare polished eyemargin can be traced all down the sides of the face and round under the eyes to nearly half-way up the back of the head; frons forming a long narrow triangle above the antennae and extending at its point more than half-way to the occiput, dull roughened black with sometimes a slight middle channel which may even shine in some lights, and bearing sparse short glistening white depressed pubescence; vertex practically bare and forming a rather shining black short triangle. Proboscis short, brownish; palpi fairly long, brown, and bearing slight brownish yellow hairs. Eyes bare, practically touching for about six or eight facets above the middle of the space between the antennae and the occiput; facets on the larger upper part conspicuously and sharply larger than those on the rather smaller lower part, and the dividing line rather curved. Antennae dull brownish-black, placed in a pit-like depression as mentioned above; basal joint very short; second joint also short and transverse, almost bare; third joint subulate, about four times as long as broad at base and slightly diminishing towards its tip but still ending very bluntly and with any trace of a terminal style or arista concealed in a sort of pit.

Thorax dull black, almost shagreened, and bearing exceedingly fine but fairly abundant scale-like greyish pubescence; humeri at the extreme hind angle, and the postalar calli more extensively, usually chestnut; pleurae rather shining because their punctation is less coarse but with their pubescence longer and more distinct, until the sternopleurae become still more shining and their pale grey pubescence fairly obvious; pteropleurae polished black and quite bare. Scutellum similar to the disc of thorax and usually chestnut on the underside, but all these chestnut markings often very obscure.

Abdomen longer than the thorax, flattened on the disc, shining black especially about the sides; 2nd to 4th segments about equal in width, the 1st being rather narrower, and the 5th and 6th diminishing in width towards the genitalia though more shelving over at the sides, the 7th short and drawn back dorsally about the middle to allow room for the swollen genitalia; 2nd segment conspicuously long, being longer than any other two together, but the others except the shorter 7th segment nearly equal in length; extreme basal margins of the 4th and 5th segments (or the membrane between them) conspicuously pure white, but the white bands not quite extending to the side margins, and a similar band is just traceable on the 6th segment; pubescence composed of such minute black bristles as to be almost imperceptible, except for a slight pale pubescence about the basal corners and some pale hairs on the genitalia. Belly shining black with chestnut reflections, bearing minute black bristles which become increasingly crowded after the 2nd segment; dorsal plate of the abdomen considerably overlapping the ventral plate. Genitalia large, with two large brownish black upper plates which push the 6th and 7th abdominal segments backwards and upwards, and these plates bear on their hindmargins a fringe of rather long pale yellow or brownish yellow hairs, while beneath them are two other large inflated plates which bear a few short pale hairs and which leave a small apical space between them from the lowest point of which a small yellowish pale haired process may protrude.

Legs shining chestnut, but the coxae and trochanters with blackish reflections, and the femora occasionally, and the tibiae (especially the hind pair) frequently with extensive darkened or even blackish markings; tarsi also considerably obscured, but chestnut at the base for at least the basal half of the first joint of the front pair, the basal three-quarters of the first joint of the middle pair, and the three basal joints of the hind pair except at their tips; femora short and thick, front pair most so, and hind pair least so; hind tibiae slightly curved but not at all dilated anywhere. Pulvilli small, brownish orange; claws small, black. Pubescence slight and all pale, forming distinct fringes behind the anterior femora, and a delicate thin fringe of longish pale hairs behind the basal half or more of the hind tibiae; no spurs present, but bristly almost spur-like hairs exist at the tip of all tibiae.

Wings with a faint brownish tinge; veins brown and strongly marked, though the lower one from the discal cell (= the upper branch of the postical fork) and the anal vein do not quite reach the wing-margin; costal vein finishing before the wing-tip and not continued as an ambient vein; upper branch of the cubital fork about two-thirds the length of the lower branch, and ending in the costa about half-way between the radial vein and the lower branch of the fork; subcostal vein stouter than the others and more surrounded with brown. Squamae (alar) small, blackish grey, with a very short grey fringe; thoracal pair absent. Halteres with a large knob occasionally all white, but more commonly white with the upper part brown, or chestnut brown with the upper part blackish, or all dull orange or brown more or less darkened, but with the rather short stem always darkened.

♀. Very similar to the male, but the frons about one-fifth the width of the width of the head; the frons has the narrow sidemargins shining and slightly curved so that it is slightly wider near the antennae than about the middle, and it is dull black but roughened by coarse punctation and striae radiating from the lower ocellus, but sometimes when the punctation is less dense it is rather shining, and usually bears a depressed middle line which is sometimes slightly shining on its middle part or even for its whole length, and this line may be widened about its middle part though not enough to form a large rounded depression, and the minute pubescence is pale; the eye-collar on the upper third of the back of the head is puffed out and shining black unless occasionally rendered dull by dense grey dust, and no tiny bristles occur down the postocular band; the raised collar is quite distinct from the hollowed-out back of the head, and diminishes downwards until about the middle where it amalgamates with the back of the head, but all the eyemargin round to the jowls still remains puffed out. Eyes with the facets all equal; in life clear brown with aeneous reflections and a dark purple band about four facets wide across from almost the front margin just above the level of the base of the antennae to almost the hindmargin. Antennae as in the male.

Thorax as in the male, but with even shorter pubescence. Abdomen flatter and without any white transverse bands; the six segments after the long second one almost equal in length and the third to the sixth with a transverse depression across the middle of each, which is also slightly visible on the sixth segment and on the second near the hindmargin; pubescence very short, but slightly longer and greyish towards the basal corners; the segments are almost parallelsided until the base of the seventh. Ovipositor small but broad and projecting from the tip of the abdomen.

Legs similar to those of the male, but the fringe behind the anterior femora almost absent though the delicate ciliation behind the hind tibiae is quite as strong. Pulvilli greyish yellow in life.

Wings with the radial vein sometimes distinctly not extending to the wingmargin, though in individual specimens it may do so in one wing but not in the other. Halteres very variable in colour, being sometimes all clear white, but often white on the underside of the knob or sometimes obscurely whitish for a moderate space on the underside and shining black on the upper side.

Length about 5 mm ♂, 6 mm ♀."

This species has not yet been definitely recorded in Australia.

SCENOPINUS NIGRA (De Geer) ♂, ♀

Hemotelus nigra De Geer, 1776, Ins. ed. Gotze **6**: 76 (10).
Scenopinus niger Verrall, 1909, British Flies **5**: 600.
niger De Geer =(*fenestralis* (pt.) Fabr.)
Scenopinus rugosus Fabr., 1794, Entom. Syst., **4**: 330.
Scenopinus tarsatus Panzer, 1806, Fauna Germ., **98**: 20.
Scenopinus ater Fallen, 1817, Dipt. Suec. Scenop., p. 5 (2).
Scenopinus nigripes Meigen, 1824, Syst. Beschr., **4**: 117.
Scenopinus fasciatus Walker, 1851, Ins. Brit., **1**: 85 (2).

Verrall writes:

"Legs blackish except on the tarsi. Frons rather shining. Eyes of the male widely separated. Hind tibiae of the male very much dilated.

A rather small very oblong fly.

♂. Frons at the vertex occupying nearly one-fifth the width of the head and gradually widening down to the antennae where it is nearly one-third the width of the head, shining black, very little punctate but with a very large rather shallow almost circular depression below the middle which almost reaches to the sides, and sometimes with a narrow longitudinal middle furrow in addition; the sides of the depression are slightly roughened; pubescence only microscopical; when viewed from above a whitish band extends on each side of the antennae down the eyemargin but is only caused by whitish dust reflections; jowls small, but bearing some dark pubescence; back of the head with a shining black raised eye-collar on the upper half which begins very thin about the middle but becomes considerably raised at the upper eye-angle; vertex obviously sunk forward between the eyes, and the ocellar space elevated. Eyes bare; facets all equal. Antennae brown, practically bare; two basal joints short, about equal in length; third joint nearly three times as long as the two basal joints together and about three times its own breadth, slightly thickened about its middle.

Thorax black, rather shining, but roughly punctate triate. Pubescence ubiquitous but consisting of only exceedingly minute adherent yellowish bristles. Scutellum with more erect pubescence.

Abdomen shining brown or brownish black, with sparse and faint punctation; the white transverse bands at the hindmargins of the fourth and fifth segments are conspicuous but narrow out before reaching the side margins, and a similar but narrower band occurs on the sixth segment and a less conspicuous whitish band on the third segment. Genitalia forming a knob which is less than half the width of the seventh abdominal segment; the pair of brown upper plates are much smaller than in *S. fenestralis* and have an inconspicuous brown fringe on their straight hindmargins; the two lower plates are large and almost overlap behind on the lower part, but leave above an almost quadrate open space which is microscopically fringed, and in the middle of which three tiny pale thread-like processes can sometimes be traced, and of them the two side processes are longer than the whitish middle one. Belly blackish.

Legs blackish, knees very faintly ferruginous, and all the tarsi reddish orange on the three basal joints except at their tips; front femora stout, and the hind femora flattened; hind tibiae very much dilated and flattened, club-shaped. Pubescence very slight and inconspicuous, but a little pale pubescence occurs behind the anterior femora, and the hind tibiae bear behind a sparse delicate fringe of longish pale hairs on rather more than the basal half.

Wings decidedly blackish brown; veins (except the subcostal) distinct though not coarse, but in other respects similar to those of *S. fenestralis*; upper branch of the cubital fork undulated, barely half as long as the straight lower branch, and ending long before mid-way between the radial vein and the lower branch. Squamae (alar) blackish brown with a brownish black margin and with a slight pale fringe. Halteres blackish, but with the top or the knob dark brown.

♀. Very similar to the male. Frons shining black, sparsely punctate on the upper part (except at the sides) but not striate near the lower ocellus, and rather wrinkled transversely on the lower half; a large conspicuous rather shallow almost circular depression occurs about the middle; sides parallel on about the upper half but afterwards gradually widening down to the antennae, though even there the frons is barely one and a half times as wide as at the vertex; a minute furrow runs down to the lower end of the depression, and a polished channelled eyemargin exists on the upper two-thirds of each side; collar at back of upper part of eyes rather narrow, fairly equal, greyish black.

Thorax black, but somewhat obscured by minute dark bristles and transverse striae on all the disc except on the middle part; humeri not at all chestnut, and the postalar calli only on the front knob. Scutellum roughened.

Abdomen shining black, but not at all brilliant; hind angles of the basal segment with some rather long though inconspicuous greyish yellow pubescence, and the hinder half of the second segment with more extended though shorter more greyish pubescence; pubescence on the rest of the abdomen blackish grey, fairly abundant, and short, though longer and more conspicuous than in *S. fenestralis.*

Legs coloured as in the male, or often with only just the base of the anterior tarsi and the three basal joints of the hind tarsi conspicuously brownish orange except at their tips; front femora only slightly thickened, and the posterior femora elongate but hardly thickened; hind tibiae shorter than the femora, straight, and not at all dilated, but with the usual delicate sparse pale fringe behind; pubescence very slight, pale behind the middle femora. Pulvilli blackish; claws black.

Wings very nigrescent, especially on the front half; upper branch of the cubital fork usually rather undulating and ending in the costa about half-way between the radial vein and the lower branch. Squamae (alar) small, dark greyish with a distinct dark margin and slight light grey fringe. Halteres blackish brown, with a shining blackish tip.

Length about 4½ mm ♂, 5 mm ♀.

This species varies a little in the amount of reddish orange or reddish brown on the tarsi and knees, but never in a way at all approximating to *S. fenestralis.*"

This species has not yet been recorded from Australia; it was found in Hawaii, but its wide distribution in the world indicates that it is likely to be present in Australia.

SCENOPINUS PAPUANA (Kröber) ♀

Omphrale papuana Kröber, 1912, Suppl. Ent. Berl. 1: 25; 1913, Ann. Hist. Nat. Mus. Hung. 11: 207, tab. 10, figs. 38, 39; tab. 11, fig. 46 (♀); 1914, Genera Insect., fasc. 161, tab. 4, figs. 26 a, b, c, d, e.

A free translation of Kröber's description is as follows:

"♀. A short, broad, stout species. Frontal stripe rather broad, not narrowing above, wrinkled, with a depressed central part becoming deepened as a groove above the antennae. Antennae placed in an excavation. The first segment of antennae very small, deep-black, second and third dusky red-brown. The third segment rather long, without an incision in front. Occiput deep black, dull. Mesonotum and scutellum black, finely punctate, rather dull, with a green sheen when viewed laterally. Between base of wing and scutellum there is on each side a comb-like red-brown callosity. The sides of thorax deep black, punctate, Halteres black-brown. The sides of thorax in proportion to length, very high, much higher than in other species of the same size.

Abdomen broad, deep black, rather dull. Margins of tergites brownish. Underside of abdomen black, more shining than the upper side.

Femora and tibiae black-brown. Femora thickened, club-like. Tarsi light reddish yellow.

Wings blackish, especially at anterior margin. Discal cell placed further towards the apex (? S.P.) of wing than in other species.

Length: 4-4.5 mm, to tip of wing 5 mm. Width of abdomen 2 mm.

Locality: Kanshirei, Formosa IV (H. Sauter leg.) and New Guinea; Simbang, Huon Gulf (Budap. Mus.).

Types: 1 ♀ Deutches Entom. Museum and 1 ♀ Budapest Museum."

This species is unknown to the author.

SCENOPINUS BIROI Kertész ♂, ♀

Scenopinus biroi Kertész, 1899, Természetr. Füz. 22: 173.
Scenopinus biroi v.d. Wulp, 1899, Tijdschr. Ent. 42: 47.
Omphrale biroi Kröber, 1913, Ann. Nat. Hist. Mus. Hung. 11: 205.

A free translation of Kertész's description is as follows:

"Similar to the European species in habitus and venation, but much smaller. Body colour shining black, with greenish tinge.

Head a little wider than thorax. Frons occupying 1/5 of the width of head, with a fine longitudinal furrow in middle and a row of dots on either side; from ocelli, two deeper longitudinal furrows run obliquely toward eye margins. Above antennae, a silvery white, shining ⊓ shaped, tuft of hairs. Antennae light brown; first segment hardly noticeable, second oval, third conical in profile. Antennae, when seen from above, curving first outwards and then inwards.

Abdominal impressions shining brown. Legs yellow. Hind femur not thickened. Wings at interior margin light brown-yellow. Halteres brown, with a lighter style.

Length: 2.5 mm.

Several specimens from Friedrich-Wilhelmshafen and Erima in New Guinea.

The family Scenopinidae was until now unknown from Indo-Malayan Archipelago. Biro writes that he caught all the specimens on windows."

The author has seen specimens from the following localities: 2 ♀♀, 5,9.iii.1931, 1 ♀ 12.i.1931, Brisbane, Q.; 1 ♀, 6.xi.25, Inglewood, Q.; 1 ♀, 27.x.1936, Brisbane (F. A. Perkins); 1 ♀, 14.x.1922, Sydney, N.S.W.; 2 ♀♀, 28,29.i.1923, Woolgoolga, N.S.W.

SCENOPINUS GLABRIFRONS Meigen ♂, ♀

Scenopinus glabrifrons Meigen, 1824, Syst. Beschr. 4: 114 (3).
Scenopinus civiculus, Hardy, 1933, Proc. Linn. Soc. N.S.W. 58: 418, fig. 2.

Hardy described this species as *S. civiculus* as follows:

"♀. Head as broad as thorax, black. Frons not quite one-third the head-width, mostly shining and smooth, but slight punctures occur in two rows, irregular in shape, each side of the median depressed line. The punctures extend over the ocellar tubercle and some slight wrinkles occur, mainly on the lower half of the frons. Behind the eyes there is a well developed flange, shining and with but few punctures, these being mainly confined to the lower half. Seen in profile the frons extends a little in front of the eyes, being broadest at the ocelli and disappears at the antennae. The oral cavity is large, leaving but little of the face to be seen, this being covered with a slightly grey tomentum. The hairs on the cheeks and elsewhere are somewhat yellowish. Antennae brown, with the third segment long, and a marked depression near the apex on the outer side. The eyes, in life, have a straight thin transverse colour band, placed so as to point slightly above the antennae. The band reaches across the eye from margin to margin.

The thorax is black, fairly densely covered with punctures and wrinkles, the slight hairs are somewhat yellowish. The scutellum is semicircular, similar to the thorax in other respects and with a subapical depression bordering the outer margin at about two-thirds its length. Below the scutellum and on the posthumeral callus, the colour is yellowish-brown.

The shining black abdomen is sparsely punctured, somewhat depressed, and about as long as the head and thorax united; it is conspicuously broader towards the apex. Legs brown, apex of the tarsi stained with black. The hyaline wings have yellowish-brown veins and the halteres have a white club. Length: 5-6 mm.

Hab.—Queensland: Brisbane, November to March, 1924, and subsequent years, 5 ♀ in my collection and 1 ♀ in that of Mr. F. A. Perkins. New South Wales: Sydney, 26th November, 1920, 1 ♀. South Australia: Adelaide, January, 1931, 1 ♀, and another without data. Mostly from windows."

The main characters of the male were mentioned in the key.

The author has seen specimens from the following localities. Brisbane, Sydney, Broken Hill, "West. Austr.", 1 ♀, Perth, W.A. (J. Clark).

The location of the type is unknown to the author, and all attempts to find it were fruitless.

SCENOPINUS PERKINSI Hardy ♀, ♂ (new)

Scenopinus perkinsi Hardy, 1942, Proc. Linn. Soc. N.S.W. 67: 202.

Hardy writes:

"♀. In life the eyes appear black, but close examination shows them to have a reddish tinge and there are no indications whatever of markings. Hair-pits occupy the whole of the frons, the eye-margins being separated only by a line, and there is also a similar median shining line very slightly raised and interrupted by a median depression in the form of a circular pit at two-thirds its length. Near the eye-margins, the frons is slightly sunken. The post-ocular border is linear, no flange being developed there.

The whole of the body is black, but brown occurs on the antennae, tibiae and tarsi, whilst faint indications of brown may also occur on the femora; in other respects the fly is quite typical of the genus.

Length: 4 to 5 mm.

The species differs from *S. civiculus* Hardy, the only other known species in Australia, by its much smaller size, lack of the post-ocular flange and very much narrower frons. No males belonging to this genus have been discovered in any Australian collection.

Hab.—Queensland: A series of females was collected in Brisbane, mostly by Mr. F. A. Perkins, from the windows of the University's Entomological Laboratory. It seems to be mainly a spring and summer species, as the collection dates show it to occur during most of these months, over several successive years."

The location of the type is unknown to the author.

♂ (new). Eyes separated above by a very thin line. Lower facets distinctly smaller than the upper ones. Antennae extremely short, third joint pear-like. Mesonotum with very few microscopic hairs, slightly shining. Halteres and legs (except yellowish tarsi) nearly black. Wings slightly infuscated. Abdomen black, with very narrow, whitish fasciae at some incisions of the tergites.

2 ♂♂, 1 ♀, emerged 12.vi.1950, Wollstonecraft, near Sydney, N.S.W. (K. A. Hindwood); 1 ♀, 9.ii.1948, Brisbane, Q. (K. R. Norris).

Genus SCENOPINULA, gen. nov.

Generotype *S. pallidipennis*, sp. nov.

Differs from *Scenopinus* in structure of frons and in venation.

The frons very swollen, in profile distinctly protruding, whole of its surface covered with small tubercles, parafrontalia much lower than the very elevated middle stripe.

Vein m_1 parallel, over the whole of its length, to the common stem of r_4 and r_5 and to r_5 itself. Cross vein r-m situated extremely close to apex of discal cell, the distance being much smaller than the vein itself. Vein r_4 very short, only slightly longer than cross vein r-m, forming a large angle with r_5. Discal cell very narrow and short, as long as the lower basal cell. Venation extremely weak.

SCENOPINULA PALLIDIPENNIS, sp. nov. ♀

Whole body black, halteres yellowish white; hind margins of the 2nd-7th tergites and sternites with very narrow, yellowish cross bands; hind margins of the 1st and 8th tergites and sternites without yellowish bands. Tarsi, postalar calli, and knees brownish.

Head, mesonotum, and scutellum nearly nude; abdomen with very short and numerous, whitish hairs, visible only under a lens.

Vertex occupying about one-third of head width. Ocelli distinct; ocellar triangle situated very high, occupying about half the width of vertex. Facets comparatively large, of equal size. Mouth cavity oval, deeply sunken, with quite reduced proboscis and palpi; antennae hanging over the apex of mouth cavity. Viewed from below the frons appears as a large tubercle. Distance between external corners of eyes very large, nearly equal to double the longitudinal diameter of eye (viewed also from below). Antennae very short, only slightly longer than ocellar triangle. The upper part of occiput not visible when head viewed from the front.

Mesonotum nude, black, shining; a large convexity above the base of wing. Halteres with a very large, massive knob, nearly twice as long as the narrow basal part.

Wings quite hyaline, veins colourless, very weak, and indistinct. Discal cell very narrow and small, as long as lower basal cell and distinctly narrower. Anal cell with petiole as long as the vein closing it. Cross vein *r-m* comparatively large, twice as long as vein closing the discal cell, or the distance from *r-m* to the apex of this cell; cross vein *r-m* placed vertically. First posterior cell parallel-sided, extremely broad. Legs black, with very short, whitish hairs.

Abdomen shining above and below, flat, of a typical *Scenopinus* form.

Length of body 2 mm, of wing 1.5 mm.

1 ♀ (type), 18.xi.1949, 8 miles S. of Lake Cobham, N.S.W. (S. J. Paramonov).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Genus RIEKIELLA, gen. nov.

Generotype *R. bicornis*, sp. nov.

Closely related to *Scenopinus*, but easily distinguished by: (1) abnormal venation, (2) structure of ovipositor, and (3) structure of 3rd antennal joint.

Frons extremely broad, with longitudinal median sulcus converging towards the antennae. Vertex occupying at least half of head width. Antennae short, 3rd joint ovoid, but very elongate, at apex regularly excavated, with 2 "horns".

Thorax nearly bare. Legs and wings as in *Scenopinus*, but vein m_1 not reaching hind margin of wing, the distance from margin being as long as vein r_4; thus 1st posterior cell is open.

Abdomen as in *Scenopinus*, but the 8th segment very elongate, about twice as long as 7th segment, much longer than broad (in *Scenopinus* it is short and much broader than long). Underside of the 8th segment keeled and attenuated into a single spine; ovipositor "sui generis" consists of 2 cerci-like prolongations protruding as far as the 8th sternite.

This genus is named in honour of Mr. E. F. Riek, to whom the author is indebted for many interesting new flies.

RIEKIELLA BICORNIS, sp. nov.

Ground colour of body brown, but specimen looks as if freshly emerged and is possibly as a rule darker. Ocellar triangle comparatively large, situated rather high in comparison with the rest of frons, occipital part nearby also situated high. Frons distinctly converging towards antennae, with a median sulcus and some short, yellowish hairs, nearly bare. Facets comparatively large, but of equal size. Occipital part in area of vertex appears as a high inflation, having the form of a very broad "V". In profile the occipital part is not broad. Mouth cavity deeply sunken, with a longitudinal furrow; proboscis and palpi very rudimentary. Third antennal joint at least twice as long as both basal joints together, pear-like in profile, very broad, but at apex with 2 acute prolongations, separated by an excavation. Cheeks in profile nearly absent.

Thorax of same dull brown colour as frons, but humeral and postalar calli yellowish. Mesonotum with hairs similar to those on frons, nearly bare. Legs yellow, femora darker, last 2 joints of all tarsi also darker. Halteres yellow, knob very large, comprising the greater part of the halteres.

Wings hyaline, with yellowish veins. Vein r_5 running exactly into apex of wing. Vein r_4 situated midway between cross vein *r-m*, and the apex of wing, nearly straight, at an angle of 45°. Cross vein *r-m* at end of 2nd third of discal cell.

Abdomen slightly shiny, elongate, with proportions as in *Scenopinus*, nearly bare; 8th segment alone with some hairs on apex; this segment at least as long as 2 preceding combined.

Length of body 3 mm, of wing 2 mm.

1 ♀ (type), 27.ix.1950, 10 miles S. Bowen, Queensland (E. F. Riek).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

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FOSSIL INSECTS FROM THE TRIASSIC BEDS AT MT. CROSBY, QUEENSLAND

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(*Manuscript received October* 8, 1954)

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Summary

The fossil Hymenoptera, Mecoptera, Orthoptera, and orders of insects related to these are described from the Triassic beds at Mt. Crosby, Queensland. The record of Hymenoptera extends considerably the time range of the order. Mecoptera, Neuroptera, and Trichoptera are abundant but Diptera and Lepidoptera are absent. There are many Orthoptera (Saltatoria) but only fragmentary remains of Protorthoptera, Perlaria, and Odonata. The assemblage of insects shows none of the problematical types of the Permian. Many of the forms recorded are described in new species and genera.

INTRODUCTION

The Mt. Crosby insect bed lies almost at the bottom of the Ipswich Series. Its stratigraphical relationships have been outlined by Tindale (1945). The Denmark Hill bed lies almost at the top of the same Series so that there is a considerable time gap between these two insect-bearing beds.

The insect-bearing horizon at Mt. Crosby has been traced by various workers for some distance in the field and insect remains collected from different sites. As the insect-bearing horizons are all more or less contemporaneous they are considered in this study as belonging merely to

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the Mt. Crosby insect bed of the Ipswich series of Triassic age. In all, about 1000 recognizable insect fossils have been obtained from this bed. The material is preserved in the University of Queensland, Department of Geology collection. The reference numbers used are those of that collection.

The order Blattaria dominates the fauna, with about 50 per cent. of the specimens being referred to it. This is abnormally high and probably reflects a specialized environment in this region during Triassic times. The climatic conditions prevailing and the manner of deposition of the horizon have not been fully worked out. The Homoptera-Psocoptera and the mecopteroid orders form the other main elements of the fauna, each constituting about 20 per cent. of the total insects. The orthopteroid orders and the Coleoptera each constitute about 5 per cent. of the fauna. Other orders are rare or entirely unrepresented in the present collection. The only one with recognizable specimens preserved is the Hymenoptera of which there are two well-preserved specimens.

The Blattaria are represented by many diverse types but, as a detailed examination has not been made, little further can be said concerning them. Their abundance is all the more surprising when one considers their complete absence from the Upper Permian of Belmont, New South Wales.

The Homoptera-Psocoptera assemblage is also very diverse and it contains possibly both the largest and smallest insects in the horizon.

The mecopteroid orders are represented by abundant Mecoptera, Neuroptera (Planipennia), and Trichoptera. Diptera and Lepidoptera have not been recognized. The Mecoptera all belong to the normal Eumecoptera, with the exception of one species which is referred to the Protodiptera.

The mecopteroid fauna shows its origin from that of the Upper Permian of Belmont. In the order Mecoptera many of the diverse types have either died out or are dying out and we are left with fewer lines which evolve into the Recent groups. The Trichoptera and Neuroptera were only poorly represented in the Upper Permian and in the Triassic they have diversified, producing types more clearly allied to Recent families.

The Coleoptera are preserved mainly as elytra. The classification of these elytra is very problematical but they do indicate to some extent the relative development of the holometabolous orders in the fauna.

The Orthoptera are mainly of the gryllacridid type and there is a single fragment belonging to the Perlaria.

There is a surprisingly poor representation of most aquatic orders. Ephemeroptera are entirely absent. There is only a single fragment of the Perlaria and another possibly of the Odonata. The Trichoptera on the other hand are well represented. There are abundant specimens of a quite small species. This leads one to speculate on the possible habits of these early Trichoptera. If their larvae were aquatic one must consider that the other orders were still scarce at that time in this area. The alternative is to consider that the Trichoptera had not developed aquatic larvae, but bred in damp situations much as do the Mecoptera.

The assemblage of insects has a rather modern facies, with none of the problematical types of the Permian persisting. It would seem to indicate moderately wet forest conditions producing abundant cockroaches and gryllacridid Orthoptera in the decaying leaves of the forest floor and under the bark of the trees, Mecoptera-Neuroptera in the more low-lying regions, and Trichoptera more closely confined to the stream beds. Homoptera would be present on the foliage of plants. Occasional dragonflies and wasps would occur amongst the vegetation, the former probably to "hang-up", the latter seeking a site for egg-laying.

The present paper considers the orders Hymenoptera, Mecoptera, Trichoptera, Neuroptera, Orthoptera (Saltatoria), Protorthoptera, Perlaria, and Odonata.

Order **HYMENOPTERA**

The earliest fossil Hymenoptera are those referred to *Pseudosirex* from the Upper Jurassic lithographic limestone of Bavaria (Carpenter 1932) and the Middle and Lower Purbeck of England and the several forms described by Martynov (1925, 1937) from the Jurassic of Turkestan, so it is particularly interesting to record the occurrence of a Triassic member of the order. It is noteworthy that the venation of the specimens from Mt. Crosby differs very little from that of the Recent genus *Macroxyela* Kirby, a genus of sawflies (family Xyelidae). *Macroxyela* does show the most generalized venation of Recent Hymenoptera but, even so, is a highly specialized derivative of the mecopteroid stock, so one must certainly look further back, at least to the Permian, for the ancestor of the order. At the present time the family Xyelidae is limited to the Holarctic region, more notably to North America. Only the more specialized families of sawflies occur in the Recent Australian fauna.

Suborder **SYMPHYTA (CHALASTOGASTRA)**

Superfamily **TENTHREDINOIDEA**

Family **XYELIDAE**

This family has the most generalized venation amongst Recent Hymenoptera. The combination, in the forewing, of a distinct *Sc* and a free R_{2+3} (or second inter-radius) separates the family from the Pamphiliidae in which there is also a distinct *Sc*.

The wing venation differs in slight respects in the genera of the family. In the forewing of *Macroxyela* Kirby, *Pleroneura* Konow, and *Odontophyes* Konow, *Sc* is free right to the base of the wing while in *Xyela* Dalman it is fused with *R* over the basal half or so. The structure of the antenna is used to a large extent in the separation of the Recent genera so the generic placing of the fossil species can only be provisional.

Genus ARCHEXYELA, gen. nov.

Genotype *Archexyela crosbyi*, sp. nov.

Forewing: Related to the Recent *Macroxyela*, but the apical crossvein from the pterostigma to *Rs* passes to the upper branch (R_{2+3}), and not to the stem, of *Rs*. *Sc* is free to the base of the wing. Stem of the media slopes towards the apex of the wing.

ARCHEXYELA CROSBYI, sp. nov.

Fig. 1

Forewing: Wing complete except for the anal area; length 9.0 mm; venation with *Sc* free to the base of the wing, crossvein from near its apex to *R* not distinct; *Cu* arising close to the base; stem of *M* sloping towards the apex; venation strong over the basal half of the wing, weak over the apical portion except for the pterostigma and the costal border including the ends of R_{2+3} and R_{4+5}.

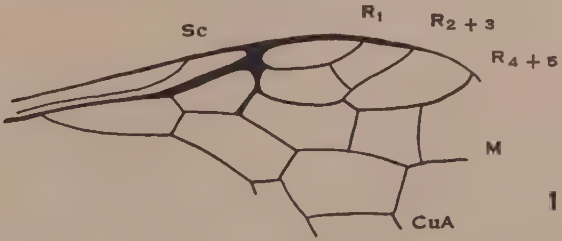


Fig. 1.—C2232, holotype of *Archexyela crosbyi*, sp. nov. *c.* × 6.

Type.—Holotype, C2232, in the University of Queensland, Department of Geology collection.

Type Locality.—Mt. Crosby Insect Bed, Ipswich Series, Triassic.

There is a second specimen, C2233, and counterpart, C2234, in the same collection as the holotype, preserving only the portion with stronger venation.

The species, though of very great interest, does nothing to elucidate the origin of the Hymenoptera, but does indicate that true Hymenoptera must have been present at least in the Upper Permian.

Order MECOPTERA

The Mecoptera are nearly all highly evolved types and belong principally to the Eumecoptera, though one species is considered in the more advanced Protodiptera. The Permopanorpidae, with many branched veins, are poorly represented and there is only a single species of the

Mesochoristidae, though this is quite common. The Orthophlebiidae are abundant in the fauna. The Neorthophlebiidae are also important and another two families, the Xenochristidae and Mesopanorpodidae, are represented. The rather small protodipteron is fairly well represented.

Suborder **EUMECOPTERA**

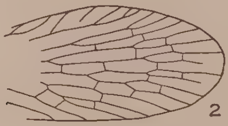
Family **PERMOPANORPIDAE** Tillyard

There is only a single described genus, *Permopanorpa* Tillyard, from the Lower Permian of Kansas (Carpenter 1930) considered here to belong in the family. Two new genera from these Triassic beds are placed in this family, but one of them only provisionally.

Genus NEOPERMOPANORPA, gen. nov.

Genotype *Neopermopanorpa mesembria,* sp. nov.

Forewing: Similar to *Permopanorpa,* but with a 7-branched media, M_4 with a strong fork; *Sc* forked near apex; well-developed pterostigma with weak branches from R_1; *Rs* 7-branched, probably a little variable; *CuA* simple, *CuP* only partly preserved; anals not preserved.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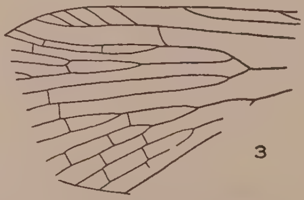
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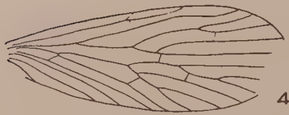
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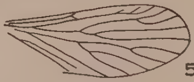
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All figures *c.* × 4.

Fig. 2.—C643, holotype of *Neopermopanorpa mesembria,* sp. nov.

Fig. 3.—C1043-4, holotype of *Xenopanorpa didymovena,* sp. nov.

Fig. 4.—C2248, forewing of *Mesochorista proavita* Tillyard.

Fig. 5.—C1595, hindwing of *M. proavita* Tillyard.

NEOPERMOPANORPA MESEMBRIA, sp. nov.

Plate 2, Fig. 1; Fig. 2

Forewing: Wing of rather large size, apex evenly rounded, widest at pterostigma; *Sc* forked at apex, not preserved basad of the fork, almost reaching pterostigma; pterostigma large, very sharply defined, R_1 bent in this region and with weak branches to wing margin; *Rs* 7-branched, regularly dichotomic, R_{2+3} forking after R_{4+5} and all but R_3 forking again towards wing margin; M 7-branched, M_{3+4} forking before M_{1+2}, M_4 also forking before M_{1+2}, so that its branches are long, extra forks also on M_1 and M_2 but none on M_3; the M_{3+4} portion has the typical mesochoristid appearance, CuA somewhat curved near wing margin and with 2 strong crossveins, 1 to M_4, the other to M_{4b}; CuP preserved only at apex, there converging slightly towards CuA; anals not preserved.

Length of fragment 7.5 mm, indicating a total length of 12 or 13 mm, as in specimen C1937.

Type.—C643 and counterpart C642 in the University of Queensland, Department of Geology collection.

Additional Specimens.—C1937 and counterpart C1938 show the outline of a complete wing, but a large disk, missing from the centre, obscures the forking of Rs and M. At the margin, the structure is as in the holotype, though there is doubt as to the structure of M_{3+4}. Cubito-median Y-vein distinct, arms unequal, CuA and CuP very probably simple, $1A$ and $2A$ long, simple, $3A$ apparently simple, a strong crossvein to $2A$. Sc with only the apical fork.

Genus XENOPANORPA, gen. nov.

Genotype *Xenopanorpa didymovena*, sp. nov.

Forewing: Differs markedly from *Permopanorpa* in the branching of Rs, stems of R_{2+3} and R_{4+5} both very short, with R_{2+3} branching just before R_{4+5}, Rs 7- or possibly 8-branched, not pectinate; M 7- or 8-branched, dichotomic, not perfectly preserved; Cu and anals not preserved; Sc forked near apex, basal portion not preserved.

The genus is only provisionally referred to this family, as it has a distinctive media. It does not show the subcostal structure of the Platychoristidae (Carpenter 1930), but the media has a rather similar appearance.

XENOPANORPA DIDYMOVENA, sp. nov.

Plate 2, Fig. 2; Fig. 3

Wing Fragment: Sc with the apex only preserved, forked, a crossvein to R_1 just after the forking; R_1 bent around the well-developed pterostigma and there possibly branched; Rs with numerous branches, R_{2+3} and R_{4+5} most characteristically forking very early and almost in line, R_4 and R_5 simple, at least for most of their length, R_3 forked about its middle, with R_{3a} definitely forked and R_{3b} possibly so but more distad, R_2 forking just before R_3 and these branches continuing simple to the wing margin, curved anteriad; M appearing 8-branched, but origin of all branches not preserved, 1st forking just before 1st forking of Rs, all forkings regularly dichotomic, M_{3+4} presumably forking before M_{1+2} and distal forks lying on an arc with that of M_1 most distad.

Length of fragment 11 mm, indicating a total length of about 20 mm.

Type.—C1043 and counterpart C1044 in the University of Queensland, Department of Geology collection.

There are no additional specimens.

The forking of *Rs* is very characteristic, as is also the regular dichotomic branching of *M*.

Family **MESOCHORISTIDAE** Tillyard

Only a single species of this family is recognized in these beds, but it is represented by numerous specimens. The family, though well represented in the Australian Upper Permian, by *Mesochorista* and *Parachorista,* has been replaced mainly by the more highly evolved Orthophlebiidae which forms a dominant element in the Mt. Crosby fauna.

Mesochorista proavita Tillyard was described originally from the Denmark Hill bed at the top of the Ipswich Series (Tillyard 1916). It is considered to occur also in the present fauna from the bottom of the Series, even though there is a considerable time gap between the two horizons.

Genus MESOCHORISTA Tillyard

Mesochorista Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 29.

Permochorista Tillyard, 1918, Proc. Linn. Soc. N.S.W. 42: 732.

Eoses Tindale 1945 (nomen nudum), Proc. Roy. Soc. Qd. 56: 39.

?*Petrochorista* Martynov, 1931 (in part), Trav. Mus. Geol. Acad. Sci. U.S.S.R. 8: 182.

Genotype *Mesochorista proavita* Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 30.

Forewing: *Sc* forked, 2-branched; *Rs* 4-branched; *M* 6-branched, the extra forks on M_2 and M_4; *CuA* simple; cubito-median *Y*-vein variable.

Hindwing: *Sc* shorter, simple; *R* as in forewing; *M* only 4-branched; *CuP* and *1A* fused for part of their length.

Tindale (1945) considered *Eoses* (genotype *Eoses triassica* Tindale) as a lepidopteron and so extended the known geological range of the order from the Eocene to the Triassic. This conclusion seems to be based mainly on the very oblique cubito-median crossvein towards the wing margin. This was considered by Tindale to be the anterior branch of a forked *CuA,* which fused for some distance with a simple M_4, but separated again before the wing margin. The position and direction of the cubito-median crossvein varies considerably throughout the Mesochoristidae. Sometimes it passes to *CuA* even from the stem of the M_{3+4}. From that point it occurs in every position along the stem of M_4 to a position about half way along M_{4b}. In some specimens it is vertical to *CuA,* but at other times it is somewhat oblique, and then it always slopes so that the cubital end is the more basad.

An examination of the holotype of *Eoses triassica,* particularly of the counterpart, convinces me that the oblique vein shown by Tindale between

CuA and M_4 is really part of an underlying wing. In the holotype, a small, thin, rock chip adheres to the wing and overlies the real crossvein, whereas in the fragmentary counterpart of the holotype, which preserves only the middle portion of the wing, the chip pulled out on the holotype has left a slight depression. Through this depression runs a strong vein, concave from above, not actually connected to *CuA*, and running right up to and slightly under M_4 just before its furcation.

The posterior margin of the wing is preserved only from R_5 to M_{2a} and there is no evidence of a pointed apex. The specimen figured by Tindale as a hindwing is considered as another forewing, again with much of the wing margin missing, so that its shape is not evident from the imperfect specimen.

With the above emendations *Eoses triassica* shows the normal *Mesochorista* structure. If it is still maintained that the species is a lepidopteron, then one must extend the range of the order back to the Lower Permian, for *Mesochorista* is a dominant element of the Belmont fauna (Riek 1953). But specimens of *Mesochorista* could almost be placed in the Recent genus *Chorista* Klug (Mecoptera, family Choristidae) except for the structure of *Sc*. So it is difficult to maintain that *Mesochorista* (*Eoses*) is a primitive lepidopteron, though it might conceivably be ancestral to that order.

MESOCHORISTA PROAVITA Tillyard

Plate 2, Figs. 3, 4; Figs. 4, 5

Mesochorista proavita Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 30.
Eoses triassica Tindale, 1945, Proc. Roy. Soc. Qd. 56: 39.

The type of this species was collected from Denmark Hill at the top of the Ipswich Series. The numerous specimens found in the Mount Crosby beds, at the bottom of this Series, are considered to be of this species. A full description of these Mt. Crosby fossils is given below.

Forewing: Wing of moderate to small size, varying from 8.0 to 11.0 mm, expanding over apical half, apex evenly rounded; costal space very slightly expanded towards base; *Sc* long, extending into the pterostigma, 2-branched, forked after the origin of *Rs*, on a level with first forking of *Rs*, upper branch short and transverse; an indistinct crossvein from Sc_2 to R_1 soon after the origin of the former; R_1 simple, sigmoid, rather strongly curved at base and at pterostigma; pterostigma large, well defined below, subcostal space wide over the middle of its length, *Rs* arising in the basal third of wing, 4-branched, stem straight, rather long, R_{2+3} rather strongly arched away from R_{4+5}, its stem quite long, longer than that of R_{2+3}, forked at the middle of the pterostigma, R_{4+5} forking rather early, the branches diverging rather strongly at base and then continuing almost parallel to the wing margin; *M* arising from the base, 6-branched, 1st forking just before the 1st forking of *Rs*, M_{3+4} forking very early, well before M_{1+2}, extra forks on M_2 and M_4; cubito-median *Y*-vein absent, *CuA* just touching M or slightly fused with it, CuA continuing then almost straight, only a slight curve near margin; CuP simple, weak; $1A$, $2A$, and apparently $3A$, simple; crossvein from M_{3+4} to CuA variable, generally arising from M_{4b} but sometimes even from the stem of M_{3+4}.

Additional Specimens (*Forewings*).—C2248, perfect except for the posterior border behind $3A$; C808-9, complete except for $2A$ and $3A$; C1747-8, without the apex; C1661-2, a perfect, smaller wing; C1103-4, another perfect small wing; C752, almost perfect and of small size. C841; C2048; C1888; C425-6; C2160-1; and C2156 are more fragmentary. C1561 is a forewing in which M is only 5-branched, M_2 being simple.

Hindwing: Similar to forewing, with rounded apex, but with straighter costal border and less expanded costal and subcostal spaces; Sc short, ending well before the pterostigma, a strongly oblique crossvein from near its apex to R_1; R_1 curved downwards and forked within the pterostigma; Rs 4-branched, similar to forewing in its arched R_{2+3}; M fused to CuA for some distance, with only 4 branches; CuA simple; CuP and anals not clearly preserved.

The description of the hindwing is based on C1595. C1407 and counterpart C1408 preserves only the apical third of the wing and shows clearly the forking of R_1 in the pterostigma and most of the arched R_{2+3}.

Type.—Holotype F39231 in the Australian Museum collection (specimen 32*a* of the Dunstan collection).

The holotype of *triassica* Tindale, F7853 and counterpart F7854, in the University of Queensland, Department of Geology collection.

Type Locality.—Denmark Hill, Ipswich Series, Triassic. Type locality of *triassica* is Mt. Crosby, bottom of the Ipswich Series.

The species differs from the Upper Permian *Mesochorista australica* (Tillyard) (Riek 1953), to which species it is most closely allied, by the straighter and longer stem of Rs and the more arched stem of R_{2+3}, the almost straight CuA and the absence of a distinct cubito-median Y-vein.

Family **ORTHOPHLEBIIDAE** Handlirsch

The only described Australian genus of this family is *Choristopanorpa* Riek (1950) from the Triassic of Brookvale, N.S.W. It is easily separated from *Neoparachorista*, gen. nov. described from these beds, by possessing a distinct cubito-median Y-vein.

Genus NEOPARACHORISTA, gen. nov.

Genotype *Neoparachorista perkinsi*, sp. nov.

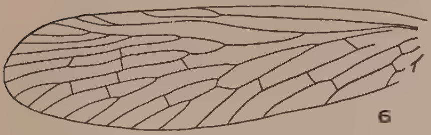
Forewing: Resembling *Parachorista* Tillyard closely in Sc and the branching of Rs, but with R_1 forked in the pterostigma; without a cubito-median Y-vein, with almost straight CuA and branching of M variable. In most species M is 5-branched, but in the genotype it is variable, generally 6-branched, with variable forkings.

The genus shows a transition from the Permian *Parachorista*. The smaller species have reduced branching of *M* (5-branched) and *Rs* only 5- or rarely 6-branched, while in the larger species some have stabilized a 5-branched media and one species has not. *Rs* is normally 7-branched in these large species. There is thus some correlation between the number of branches and size.

Hindwing: Similar to forewing but *M* with only 4 branches and *Sc* shorter and simple. *CuP* and 1*A* fused for part of their length.

NEOPARACHORISTA PERKINSI, sp. nov.

Plate 1, Figs. 1-3; Plate 2, Fig. 8; Figs. 6, 7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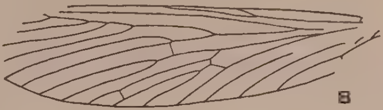
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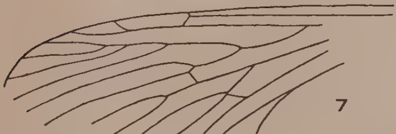
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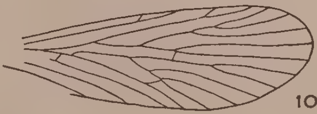
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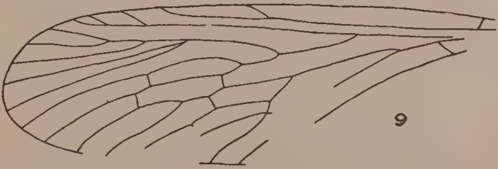
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Fig. 6.—C1897 holotype of *Neoparachorista perkinsi*, sp. nov. *c.* × 2.5.
Fig. 7.—C2145, hindwing of *N. perkinsi*. *c.* × 2.5.
Fig. 8.—C1889, holotype of *N. splendida*, sp. nov. *c.* × 2.5.
Fig. 9.—C1760, holotype of *N. semiovena*, sp. nov. *c.* × 2.5.
Fig. 10.—C2080, holotype of *N. nana*, sp. nov. *c.* × 4.

This genus is very well represented in the fauna. There are four species and more than 30 specimens, this being considerably more than those of *Mesochorista*. It differs from most other Orthophlebiidae in lacking a distinct cubito-median *Y*-vein.

Forewing: Wing large, length 24 mm, relatively narrow, costal space not expanded, apex evenly rounded; *Sc* long, 2-branched, forking a little variable, at or after the 1st forking of *Rs*, upper branch short, lower branch long, extending to the pterostigma; a crossvein from Sc_2, from just after its origin, to R_1; subcostal space widest at the origin of *Rs*; humeral crossvein strongly developed, R_1 strengthened at base, gently sigmoidally curved, more strongly so at pterostigma, with 1 or 2 (generally 2) short branches to the anterior margin; pterostigma well defined, lower margin distinct; *Rs* arising in the basal third of the wing, stem of moderate length, typically 7-branched, R_{4+5} branching once, dichotomously, R_{2+3} forming a close pectinate series, first forking of R_{2+3} generally slightly after R_{4+5}, but occasionally on a level with it (in the holotype R_5 has a terminal twigging); *M* arising from base, typically 6-branched, first forking slightly before first forking of *Rs*, with M_{3+4} forking before M_{1+2}, extra forks on M_2 and M_4; cubito-median *Y*-vein absent as *CuA* fuses with *M* for some distance; *CuA* simple, almost straight after separating from *M* but a slight curve towards wing margin, a distinct crossvein from *CuA* to M_4 almost at its origin; *CuP* simple, weak; 1*A*, 2*A* simple, zigzagged, 3*A* apparently simple.

Type.—Holotype forewing C1897 and counterpart C1898 in the University of Queensland, Department of Geology collection.

Additional Specimens.—In C735-6 and counterpart C734, *M* is 6-branched, but M_2 is simple and M_3 forked towards the margin; R_{2+3} forks on a level with R_{4+5}. In C1907, which is almost a complete wing, the median field is quite abnormal. As can be seen from the plate, an oblique crossvein from M_3 to M_{1+2} is strongly developed, so that M_{1+2} appears to arise from M_3, which itself has a small terminal twigging. M_2 is simple and M_4 appears to be forked, though this portion of the wing is obscured. The oblique crossvein from *CuA* to M_4 is clearly defined. The crossvein from *Sc* to R_1 occurs just before the forking of *Sc*, which forks rather late. C1640 and counterpart C1641 is a normal wing lacking only the extreme apex. It has a 6-branched media. C1718 and counterpart C1719; C1808 and counterpart C1809; and C1770 and counterpart C1771 are more fragmentary. C615 and counterpart C616; C843; C439 and counterpart C440; C1001 and counterpart C1002; C1977 and counterpart C1978; and C1168 and counterpart C1169 are referred only doubtfully to this species.

The forking of *M* is thus variable, but there seems to be an unstable 6-branched condition.

C2145 and counterpart C2144 is a well-preserved hindwing. C1943-4; C943-4 and C1985-6 are considered very doubtfully as fragmentary hindwings.

Hindwing: Costal space slightly expanded towards the base; *Sc* simple, long, ending a little before the pterostigma, with a crossvein to R_1; R_1 forked in the small but distinct pterostigma; *Rs* similar in structure to the forewing; *M* only 4-branched; *CuA* simple; *CuP* and 1*A* fused until rather close to the wing margin.

NEOPARACHORISTA SPLENDIDA, sp. nov.

Plate 1, Fig. 4; Fig. 8

Forewing: Wing large, length 20 mm, relatively narrow; costal margin almost straight, slightly arched near base; *Sc* forking about the middle of the stem of *Rs*; R_1 slightly forked in the pterostigma; *Rs* arising in the basal quarter, closer to the base than in *perkinsi*, 6-branched, with a small terminal twigging, R_{2+3} forking well after R_{4+5}, forming a pectinate series; M 5-branched, extra branch on M_4; CuA and M fused for some distance; CuP and anals normal, but $3A$ not preserved.

Type.—Holotype forewing C1889 and counterpart C1890 in the University of Queensland, Department of Geology collection.

There are no additional specimens. The species differs from *perkinsi* in the 5-branched media, the late branching of R_{2+3}, and early forking of Sc.

NEOPARACHORISTA SEMIOVENA, sp. nov.

Plate 1, Fig. 5; Fig. 9

Forewing: Wing large, length 25 mm, relatively broad, apex widely rounded, costal margin almost straight, slightly arched near base. Sc as in genotype; R_1 almost straight, gently curved at pterostigma and there with 2 short branches to the costal margin; Rs arising in the basal third, stem of moderate length, R_{2+3} arched strongly away from R_{4+5}, with its stem rather long, about as long as that of Rs, forking well after forking of R_{4+5}, forming a pectinate series of 5 branches similar to genotype (in holotype 1st branch arises from the stem at the same point as the 2nd branch but in a second specimen it is normal); R_{4+5} with only 1 forking; M arising from base, angled after fusion with CuA, 5-branched, 1st forking just before the 1st forking of Rs, M_{3+4} forking well before forking of M_{1+2}, extra fork on M_4; CuA fused to M for a great distance, rather angled after this fusion, but then with only a slight curve near wing margin; CuP simple, weak; anals not preserved.

Type.—Holotype forewing C1760 and counterpart C1759 in the University of Queensland, Department of Geology collection.

Additional Specimens.—C2152-3 is complete except for the base but it is rather distorted. C732 and C733 (glued together) and counterpart C731 is more fragmentary.

This species differs from *perkinsi* in the very arched nature of the stem of R_{2+3} at its furcation from R_{4+5} and in the relatively much broader wing, which is as long as *perkinsi*. The media has only 5 branches.

NEOPARACHORISTA NANA, sp. nov.

Fig. 10

Forewing: Wing of moderate size, length 12 mm, relatively very small compared with the other species of the genus, costal space not expanded, apex evenly rounded; Sc long, 2-branched, forking after the origin of Rs, in structure similar to genotype but relatively a little shorter; R_1 only very gently curved, with at least 1, and possibly 2, short branches to the costal margin from within the pterostigma; subcostal space widest at the origin of Rs and towards base; Rs arising in basal third of wing, 5-branched, stem rather short, R_{2+3} arched a little away from R_{4+5}, forking after R_{4+5}, with 3 branches, R_3 simple and R_2 forked, R_{4+5} forked only once; *M* arising from base, rather strongly arched after its fusion with *CuA*, 5-branched, forking just before 1st forking of *Rs*, with M_{3+4} forking well before M_{1+2}, extra fork on M_4 which forks almost immediately, all branches long; no cubito-median *Y*-vein, *CuA* fused to *M* for a considerable distance, simple, almost straight; *CuP* simple, weak; 1*A* and 2*A* simple, 3*A* not preserved.

Type.—Holotype C2080 and counterpart C2081 in the University of Queensland, Department of Geology collection.

Additional Specimens.—Another 10 specimens are referred to this species. C2146-7 is a well-preserved specimen, slightly larger than most (length 14 mm), and with an extra twigging on R_{2+3}, so that *Rs* is 6-branched. C1012 and counterpart C1011 together form a wing perfect except for the anals. C1911-2; C2148-9; C1751-2; C2082; C2154-5; and C2150-1 are more fragmentary. C634-5; and C1728-9 are possibly hind-wings, as they have a media which is only 4-branched, but they lack the diagnostic anal and costal areas.

This species has a branching of *Rs* and *M* similar to that of *Mesopanorpa* Handlirsch, but differs from that genus in the absence of a cubito-median *Y*-vein and in the structure of *Sc*.

Family **NEORTHOPHLEBIIDAE** Handlirsch

This family is represented in the Lias of the northern hemisphere by *Neorthophlebia* Handlirsch, *Protobittacus* Tillyard, and *Probittacus* Martynov. A new genus is recorded here from the Triassic of Mt. Crosby. This genus is most closely allied to *Protobittacus* (Tillyard 1933). The family is separated from the Orthophlebiidae mainly on the branching of *Rs*, but the structure of *Sc* is also different.

It bears a superficial resemblance to the Recent Choristidae but has a strongly narrowed wing base, straight costal margin and marked fusion between *CuA* and *M* towards the base.

Genus ARCHEBITTACUS, gen. nov.

Genotype *Archebittacus exilis*, sp. nov.

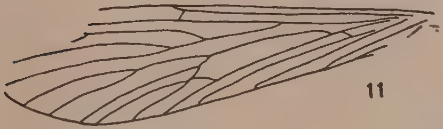
Differing from *Protobittacus* Tillyard of the Lias of England mainly in the more narrowed base and in 3*A* being either completely absent or very short. The forking of M_4 is normal, there being a distinct stem to this vein before it branches.

ARCHEBITTACUS EXILIS, sp. nov.

Plate 2, Figs. 5-7; Figs. 11, 12

Forewing: Wing rather large, length 16 mm; apex evenly rounded, base markedly narrowed, costal margin almost straight; costal space narrow; *Sc* close to the costal border, more than half the wing length, with an oblique crossvein to R_1 from close to its apex; R_1 forked in the large, sharply defined pterostigma; *Rs* 4-branched, normal, but R_{2+3} arching up towards R_1; *M* arising at base, fused to *CuA* for a short distance, 5-branched, with the extra branch on M_4, the 3 lower branches all long; *CuA* connected to the stem of M_4 by a transverse crossvein; *CuP* approaching close to *CuA* near its apex; 1*A* and 2*A* long, but 2*A* considerably shorter than 1*A*, more or less parallel to *CuP*; 3*A* not preserved, if present, then extremely short and transverse.

Hindwing: Description based on C2091-2, which lacks the apical third. Costal margin straight, costal space very narrow; *Sc* ending on the costal margin level with the 1st forking of *Rs*; the stems only of R_{2+3} and R_{4+5} preserved; *M* fused with *CuA* at base, 4-branched, or at least with M_3 and M_4 simple; *CuP* and 1*A* fused until about the middle of their lengths; a strong crossvein from 2*A* to 1*A* just after its freeing from *CuP*; 2*A* and 3*A* simple, connected by a crossvein, 3*A* quite short.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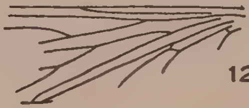
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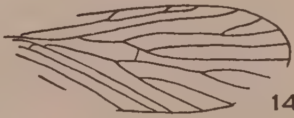
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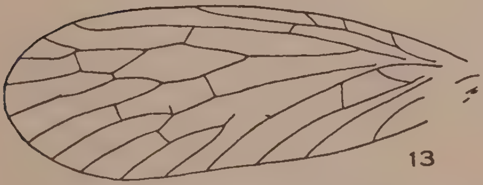
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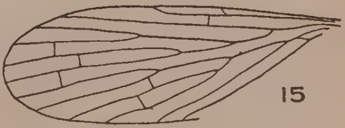
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Fig. 11.—C2139, holotype of *Archebittacus exilis*, sp. nov. *c.* × 4.
Fig. 12.—C2091, hindwing of *A. exilis*. *c.* × 4.
Fig. 13.—C2115, holotype of *Xenochoristella hillae*, sp. nov. *c.* × 7.
Fig. 14.—C2172, holotype of *Prochoristella whitehousei*, sp. nov. *c.* × 8.
Fig. 15.—C1054, holotype of *Mesotanyderus jonesi*, sp. nov. *c.* × 8.

Type.—Holotype C2139, and counterpart C2140, a perfect right forewing, in the University of Queensland, Department of Geology collection.

Additional Specimens.—C1545-6 is the complete apical two-thirds of a wing; C1495-6 has the apex and the anal veins missing. C911-2 is more fragmentary.

With the extreme reduction of $3A$ in the forewing, this species approaches the Bittacidae, differing, in addition, chiefly in the 5-branched media.

Family **XENOCHORISTIDAE** Riek

This family was erected for a Permian genus with a 3-branched Sc and with Rs and M normally 4-branched. A second genus is described from these beds. It differs in having an added crossvein in the costal space and in the reduced cubito-median Y-vein.

The family is considered a possible derivative of the Agetopanorpidae (Carpenter 1930).

Genus XENOCHORISTELLA, gen. nov.

Genotype *Xenochoristella hillae*, sp. nov.

Forewing: Differing from *Xenochorista* Riek in that the 3-branched Sc has a distinct crossvein to the costal margin from between the 1st and 2nd branches. Cubito-median Y-vein with the arms unequal.

XENOCHORISTELLA HILLAE, sp. nov.

Plate 2, Fig. 9; Fig. 13

Forewing: Wing of moderate size, length 10-11 mm, costal margin moderately expanded, apex evenly rounded, greatest width somewhat beyond the middle; Sc moderately long, extending almost to the pterostigma, 3-branched, 1st branch at junction of basal and middle thirds of the vein, upper branches both short, between the 1st and 2nd branches a distinct crossvein; a crossvein from the apical branch of Sc, soon after its origin, to R_1, this crossvein lying in the basal half of the wing; R_1 simple or possibly forked in pterostigma, only gently curved, most obviously so at the pterostigma; pterostigma large, clearly defined; Rs arising in the basal quarter of the wing; 5-branched, with a small terminal twigging on R_2, stems of R_{2+3} and R_{4+5} both long, R_{4+5} forking just before R_{2+3}; a number of strong crossveins in this area of the wing, one from stem R_{2+3} to R_1, one between R_3 and R_4, one from stem R_{4+5} to stem M_{1+2} and weaker, though distinct, ones more distad; M arising from the base or almost so, 4-branched, 1st forking level with the 1st forking of Rs, M_{3+4} forking only a little in advance of M_{1+2}; cubito-median Y-vein distinct, arms unequal, that from Cu much the longer; CuA simple, curved near margin, where possibly there was a crossvein to M_{3+4}; CuP simple, weak, the crossvein to CuA rather basad, in basal third of their lengths; $1A$, $2A$ simple, rather long, $3A$ short, apparently simple.

Type.—Holotype forewing C2115 in the University of Queensland, Department of Geology collection.

There are no additional specimens.

Family **MESOPANORPODIDAE** Tillyard

Forewing: *M* 4-branched; *Rs* 4-branched; *Sc* 2-branched; cubito-median *Y*-vein variable.

A number of species whose affinities are not clearly known have been placed in this family. They all possess venation reduced almost to its simplest. There is one species belonging to this group in these beds. It is placed in the genus *Prochoristella* Riek, which contains several Upper Permian species.

Genus PROCHORISTELLA Riek

Prochoristella Riek, 1953, Rec. Austr. Mus. 23: 71.

Genotype *Prochoristella megaloprepia* Riek, 1953, loc. cit.

Forewing: *Sc* long, forked, 2-branched; R_1 simple; pterostigma well developed; *Rs* 4-branched; *M* 4-branched; cubito-median *Y*-vein variable, arms equal or *CuA* and *M* fused; *CuA* and *CuP* simple; 1*A* and 2*A* simple, 3*A* apparently so.

PROCHORISTELLA WHITEHOUSEI, sp. nov.

Plate 2, Fig. 13; Fig. 14

Forewing: Wing resembling that of *Mesochorista proavita* Tillyard, except that *M* is only 4-branched and the wing is smaller (length 5.5 mm); costal margin convex, costal space somewhat expanded; R_1 distinctly curved near its base so that there the subcostal space is wide; *Rs* 4-branched, with R_{2+3} slightly arched and forking rather late, close to the wing margin; *M* 4-branched, normal; *CuA* and *M* fused for a short distance near the base, with *M* arching away slightly from *CuA*; *CuP* weak; 1*A* and 2*A* parallel to *CuP*, 3*A* and extreme base not preserved.

Type.—Holotype C2172 and counterpart C2173 in the University of Queensland, Department of Geology collection.

There are no additional specimens.

The species resembles *Mesochorista* Tillyard rather closely, showing a very similar structure to *Rs* but with more fusion between *CuA* and *M* and with *M* only 4-branched. On this last character one might consider it the hindwing of *Mesochorista*, but there is no fusion between *CuP* and 1*A*, and *Sc* and the costal margin are normal for a forewing.

Suborder **PROTODIPTERA**

Family **PERMOTANYDERIDAE** Riek

Forewing: *Sc* long and simple, close to the costal margin; pterostigma well developed; *Rs* 4-branched; *M* 4-branched; *CuA* simple; cubito-median *Y*-vein variable; *Sc*, *R*, and *M* more or less fused for a short distance basally.

The family was erected for two Permian genera (Riek 1953) and is expanded to include a third from the Triassic, which, however, has a rather different structure. The cubito-median Y-vein is absent, so this genus cannot be considered on the line of the true Diptera.

Genus MESOTANYDERUS, gen. nov.

Genotype *Mesotanyderus jonesi*, sp. nov.

Differs from *Permotanyderus* Riek in the longer, narrower wing, more basad origin of *Rs*, and in the absence of a cubito-median Y-vein; anal veins apparently 3, with $2A$ and $3A$ short; stem of R strengthened at base and with Sc and M fused with it; R strongly angled at this point; crossveins of limited number over the apical half.

MESOTANYDERUS JONESI, sp. nov.

Plate 2, Fig. 14; Fig. 15

Forewing: Wing small, length 6.5 to 8.0 mm, relatively narrow, costal margin almost straight, apex rounded, tapering slightly to base, greatest width beyond the middle; costal margin strengthened, appearing thicker than any of the veins; Sc long, simple, close to the costal margin, reaching into pterostigma, ending on costal margin, with a short crossvein from about the middle of its length to the costal margin, a more pronounced crossvein from just beyond this to R_1; humeral crossvein very short, distinct; R_1 strengthened at base, decidedly kinked beyond this point, gently curved to the origin of *Rs*, then almost straight to wing margin, not bent around the well-developed pterostigma; *Rs* arising in the basal quarter of wing, 4-branched, all branches long, stem of *Rs* short, R_{4+5} forking before R_{2+3}; M arising in the thickened basal portion of R and there decidedly angled, 4-branched, 1st forking at a level with that of *Rs*, M_{3+4} forking almost immediately so that these branches are exceptionally long, M_{1+2} forking just after R_{4+5} so that the branches are long; no cubito-median Y-vein, M and CuA fused for some distance; CuA continuing almost straight but with slight curves near margin; CuP simple, well spaced from CuA; anals not preserved in holotype but in a second specimen apparently 3, $2A$ and $3A$ both short; wing distinctly narrowed over the cubito-anal area.

Hindwing: Based on C2085, which lacks the anterior portion of the basal half. Apex of wing rounded; *Rs* with the same 4 branches as in the forewing, but all reaching the margin above the apex of the wing; branching of M as in forewing; CuA similar; CuP and $1A$ fused for a short distance, free over their apical portions; $2A$ short, curved strongly, connected to $1A$ by a strong crossvein.

Type.—Holotype forewing C1054 and counterpart C1053 in the University of Queensland, Department of Geology collection.

Additional Specimens.—C2168-9 is complete except for the anals; C2249 is a complete wing, a little larger than the holotype, not as clearly preserved, but showing the complete outline of the wing and more of the anal area.

Order **TRICHOPTERA**

The Trichoptera are abundant and of small size. Nearly all belong to one species.

Two families of this order are recorded from these beds. The Cladochoristidae have persisted from the Upper Permian where there is a single species represented by several specimens (Riek 1953). The single species in the Mt. Crosby beds was abundant, being represented by 38 specimens.

The second family, Prorhyacophilidae, nov., contains a single monotypic genus, the species of which is based on only the holotype, which is perfectly preserved and shows a wing not very different from that of the Recent family Rhyacophilidae.

Family **CLADOCHORISTIDAE** Riek

There are two genera in this family, *Cladochorista* Tillyard from the Permian and *Cladochoristella,* gen. nov., from these Triassic beds, differing only in the number and structure of the costal veinlets.

Genus CLADOCHORISTELLA, gen. nov.

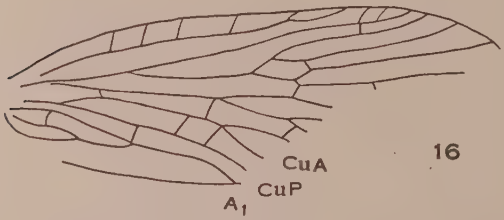
Genotype *Cladochoristella bryani,* sp. nov.

Forewing: Differing from *Cladochorista* only in the reduced crossveins in the costal area. A series of 4, spaced, almost transverse, costal veinlets (excluding the humeral crossvein and apical branch of *Sc*) ; R_1 forked in the pterostigma, 3-branched; arms of the cubito-median *Y*-vein unequal; R_{2+3} forking before R_{4+5} (occasionally slightly after).

CLADOCHORISTELLA BRYANI, sp. nov.

Plate 2, Figs. 10-12; Fig. 16

Forewing: Wing of moderate size, holotype length 12 mm but most specimens a little smaller, costal area markedly expanded basally; *Sc* long, extending into the well-marked pterostigma, giving off a series of 4, spaced, transverse, anterior branches to the wing margin, forked at its apex and with a short crossvein from Sc_2 to R_1; R_1 strongly kinked at the level of the humeral crossvein, gently curved near its apex, forked within the pterostigma, 3 or sometimes only 2 terminal branches; in the region of the origin of *Rs* the subcostal space is as wide as the costal space; stem of *Rs* long, stems of R_{2+3} and R_{4+5} very short, that of R_{2+3} slightly the shorter, all 4 branches of *Rs* very long, gently curved, notably R_2 and R_3; *M* arising from *R* very close to the base, 4-branched, the 1st forking before the 1st forking of *Rs*, with M_{3+4} forking just before the level of R_{4+5} and well before M_{1+2}; a distinct cubito-median *Y*-vein, the arms very unequal, the branch from *M* the shorter; *CuA* strongly forked, the forking extending over more than its apical third, forking before 1st forking of *Rs*; *CuP* weak, diverging a little from *CuA* and curved at apex; 1*A* curved at base, mainly almost parallel to *CuP*, 2*A* and 3*A* looped, well separated from the wing margin. Crossveins well developed, strong ones from R_2 to the pterostigma, from the furcation of *M* to stem of *CuA*, from at or just before the furcation of *CuA* to *CuP* and another, more basad, from *CuP* to 1*A* at loop of 2*A*, from 1*A* to about the middle of 2*A* and many in the distal half, notably between R_3 and R_4 and between R_5 and M_{1+2} near their bases.



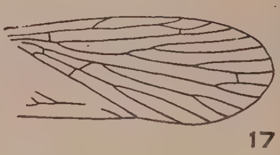


Fig. 16.—C1746, holotype of *Cladochoristella bryani*, sp. nov. *c.* × 7.
Fig. 17.—C1741, holotype of *Prorhyacophila colliveri*, sp. nov. *c.* × 8.

Type.—Holotype C1746 and counterpart C1745 in the University of Queensland, Department of Geology collection.

There are 37 additional specimens. The great majority show a structure differing little from the holotype, though M_{3+4} may fork slightly after R_{4+5} as illustrated by C2181 and counterpart C2182. In two specimens, the stem of *M* forks a little early, as illustrated by C710 and counterpart C709. C882 and counterpart C881 shows a variation of the apical forking of *Sc*, Sc_2 fusing with R_1 for a short distance instead of being connected by a crossvein. C1601 and counterpart C1602 shows R_{4+5} forking almost as early as R_{2+3} and there is an extra small twigging on M_1. C1594 shows R_{4+5} forking just before R_{2+3} and there are five additional specimens showing this condition or showing the two branching at the same level (C2174; C2178; C475-6; C695-6; C2083). C1563 is a fragmentary specimen showing M_{1+2} and M_{3+4} forking almost in line; it is referred only doubtfully to the species.

Hindwing: C1667 and counterpart C1668 is a fragmentary hindwing with a distinctly forked *Sc* ending well before R_1, which curves around the apex. The costal space is only very slightly expanded. *Rs* forks as in the forewing, *M* is only partly preserved, the forking of *CuA* is preserved, but *CuP* and the anals are missing.

Family **PRORHYACOPHILIDAE**, fam. nov.

Sc forked at apex, with only a single crossvein to the costal margin; cubito-median *Y*-vein distinct; R_{2+3} forking before R_{4+5}; *CuA* deeply forked.

The forewing, at least, is very similar to that of Recent Rhyacophilidae differing mainly in the expanded costal and subcostal spaces and primitive alignment of the veins at the base of the wing. It differs from the Liassic *Necrotauliidae* (Tillyard 1933) in the forked *Sc*, forking of *Rs*, and distinct cubito-median *Y*-vein.

Genus PRORHYACOPHILA, gen. nov.

Genotype *Prorhyacophila colliveri*, sp. nov.

Forewing: *Sc* forked at apex, with only a single, strong crossvein to the costal margin; R_1 simple; *CuA* deeply forked; *CuP* straight; a distinct cubito-median *Y*-vein.

PRORHYACOPHILA COLLIVERI, sp. nov.

Fig. 17

Forewing: Wing very small, length 5.0 mm, costal margin almost straight, not markedly expanded at base, *Sc* very long, with a strong short crossvein to the costal margin at about the middle of its length; R_1 only gently and irregularly curved, a short transverse crossvein from Sc_2 to R_1; a strong crossvein from *R* to *Sc* before the origin of *Rs*; *Rs* arising close to the base, 4-branched, stem of moderate length, R_{2+3} forking well before R_{4+5}; *M* arising from the thickened *R* almost at base, 1st forking well before the 1st forking of *Rs* but M_{1+2} and M_{3+4} both forking very late, after the forking of R_{4+5}, with M_{3+4} slightly before M_{1+2}; cubito-median *Y*-vein small, very close to the base of the wing, the arms slightly unequal; *CuA* forked over almost the apical half; *CuP* almost parallel to *CuA*, well separated from it; anals typical, looped. A strong crossvein from the middle of the stem of *CuA* to *CuP* and another more oblique one from the same point to the stem of *M*.

Type.—Holotype C1741 in the University of Queensland, Department of Geology collection.

C2179-80 is referred doubtfully to this species. The species has a typically Recent facies.

Order **NEUROPTERA (PLANIPENNIA)**

The abundant Neuroptera have proved most interesting. They have been placed in several families, not because they are so very different, but because they show marked tendencies towards Recent families. However, they are not specialized enough in most cases to be considered in the Recent families. For example, the Proberothidae and Archeosmylidae are not markedly different and might be considered in the one family, but the differences are just as marked as those between the Archeosmylidae and those forms, from these beds, considered to be true Osmylidae. The extremes, Proberothidae and Osmylidae, are very different and should undoubtedly be considered distinct. The Osmylidae grade towards the remaining family, the Osmylopsychopidae.

Of the Neuroptera of the Upper Permian of Belmont (Riek 1953) only the Archeosmylidae has persisted or, at least, is represented in the present collection. This family was possibly derived from a permithonid-type somewhat similar to *Permithone* Tillyard by increased pectination of *Rs, CuA,* and *CuP,* and prolongation of the pterostigma round the margin towards the apex. The Proberothidae could also be derived from *Permithone* by increased forking of the costal veinlets in the forewing, deep forking of *CuP*, and reduced crossveins both between R_1 and *Rs* and in the gradate series of crossveins.

Four families of Planipennia are recognized in these beds. Along with the Archeosmylidae which have persisted from the Permian (Riek 1953) one finds true Osmylidae. The new family Proberothidae seems to be directly ancestral to the Berothidae. The species previously referred to the Prohemerobiidae are better considered in a separate new family, the Osmylopsychopidae, differing from the Prohemerobiidae at least in the marked fusion between *Sc* and R_1 at their apices.

Family **PROBEROTHIDAE**, fam. nov.

Related to the Recent Berothidae, but having more crossveins and with a greater number of simple costal veinlets.

Forewing: Costal veinlets forked over the middle portion; inter-radial crossveins never more than 4; *Rs* with 4 or more branches (not counting *MA*); *CuP* deeply forked; crossveins forming an outer gradate series and an inner more irregular series.

Two monotypic genera described in this paper are placed in the family. They are separated mainly on the structure of *MA*.

The family differs from the Permosisyridae of the Russian Permian (Martynov 1933) in the more numerous branches of *Rs*, the pectinately branched *CuA* and the smaller, differently branched *MP*, but the two are rather similar. Martynov has given a slightly different interpretation of the venation in *Permosisyra* (Martynov 1933), his CuA_2 is considered to be *CuP* and *CuP* (?) is 1*A*.

Genus PROBEROTHA, gen. nov.

Genotype *Proberotha superba,* sp. nov.

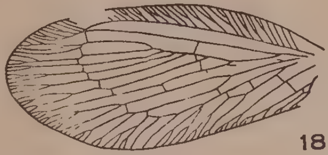
Forewing: Costal space markedly expanded over the middle portion; margin of wing almost entire; *Sc* and R_1 fused near the apex; normally 3 crossveins between R_1 and *Rs*; *MA* and *Rs* connected only by a crossvein.

This genus differs from Berothidae only in the larger number of crossveins and less completely forked series of costal veinlets in the forewing and in the presence of a free *MA*.

PROBEROTHA SUPERBA, sp. nov.

Plate 3, Fig. 1; Fig. 18

Forewing: Wing rather small, length of perfect holotype 7 mm; costal space narrowing rather rapidly towards the apex; apex rounded, margin with very slight emargination just below the apex; greatest width over the middle third; costal veinlets numerous, the first 3 or 4 simple, succeeding ones mostly forked almost to the fusion of Sc and R_1; Rs arising near the base, with 6 major branches and 3 or more shorter ones near the apex (not counting MA); M arising from the base, branching into an almost simple MA and an MP with 2 major branches; MA connected to the stem of Rs by a short oblique crossvein and so appearing more as a branch of Rs, the basal stem of MA not completely preserved, but its origin from M and portion before crossvein from Rs clear; the branches of MP each forking again towards the wing margin in addition to the terminal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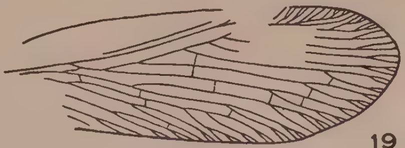
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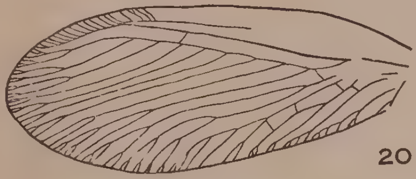
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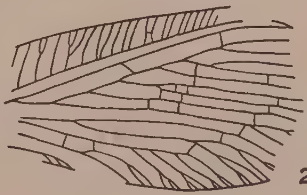
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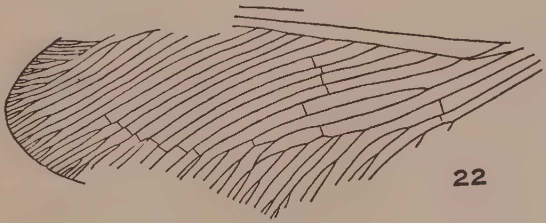
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Fig. 18.—C1404, holotype of *Proberotha superba*, sp. nov. *c.* × 7.
Fig. 19.—C2196, holotype of *Proberothella elongata*, sp. nov. *c.* × 6.
Fig. 20.—C785, holotype of *Archeosmylus stigmatus*, sp. nov. *c.* × 6.
Fig. 22.—C2189, holotype of *Lithosmylidia lineata*, sp. nov. *c.* × 4.
Fig. 21.—C907, holotype of *A. ?costalis*, sp. nov. *c.* × 6.

twigging; cubito-median *Y*-vein with distinct, subequal arms; *CuA* with 5 or more major pectinate branches; *CuP* deeply forked; anals only with end-twigging; crossveins not numerous, only 3 between R_1 and *Rs*, a complete outer gradate series between the branches of *Rs, M,* and *CuA*, and an inner irregular series between some of the branches of *Rs, M,* and *Cu.*

Type.—Holotype forewing C1404 and counterpart C2098 in the University of Queensland, Department of Geology collection.

There are a number of additional specimens. C1615 lacks the basal quarter and has slightly fewer branches to *CuA*; C1763-4 and C2060-1 are more fragmentary.

Genus PROBEROTHELLA, gen. nov.

Genotype *Proberothella elongata,* sp. nov.

Forewing: Similar to *Proberotha,* but differing in the marked fusion between *MA* and *Rs* and in the deeply forked 1*A*.

PROBEROTHELLA ELONGATA, sp. nov.

Plate 3, Fig. 2; Fig. 19

Forewing: Wing rather small, length 9 mm; costal space not clearly preserved, markedly expanded in the middle, narrowing towards the apex; *Rs* arising near the base, with 6 or 7 main branches, not counting *MA* which is fused to the stem of *Rs* for some distance, basal stem of *MA* fusing with *Rs* close to its origin; *MP* forking after the origin of *MA* from *Rs* and both branches well forked towards the margin and mostly with normal end-twigging; *CuA* with 3 or 4 terminal branches, not markedly pectinate; *CuP* deeply forked; 1*A* deeply forked, 2*A* with terminal twigging; crossveins not all clearly preserved, but outer and inner gradate series present and a few, more basad, crossveins.

Type.—Holotype forewing C2196 and counterpart C2197 in the University of Queensland, Department of Geology collection.

There are two additional specimens. C1021-2 shows the apex and posterior half of a wing and C1927-8 shows the apical third of a wing. In both these specimens the structure is so close to that of the holotype that there can be no doubt of their determination.

The species is clearly differentiated on the structure of 1*A*, but also on *CuA*, M_{1+2} and the branching of *Rs*.

Family **ARCHEOSMYLIDAE** Riek

Resembling Recent Osmylidae, more especially Protosmylinae, but without regularly arranged gradate crossveins and with simpler *CuP* and anal veins. *CuP* rather deeply forked but not pectinately branched; anal veins simple for most of their length, but with short pectinate branches near the wing margin.

There is only a single genus, recorded originally from the Upper Permian of Belmont (Riek 1953), but with additional species in these Triassic beds of Mt. Crosby.

Genus ARCHEOSMYLUS Riek

Archeosmylus Riek, 1953, Rec. Austr. Mus. 23: 85.

Genotype *Archeosmylus pectinatus* Riek, 1953, op. cit. 86.

Forewing: *Sc* and R_1 fused; pterostigma long and curved round towards the apex; *Rs* with rather numerous branches (8 or 9); *Rs* and *MA* fused for a short distance, with the proximal portion of *MA* appearing almost transverse; *CuP* deeply forked; anals simple except for short pectinate branches near the margin.

ARCHEOSMYLUS STIGMATUS, sp. nov.

Plate 3, Fig. 3; Fig. 20

Forewing: Wing small, length 10 mm; apex rounded or very slightly pointed; costal space markedly expanded towards the base, narrowed towards the apex, greatest width well beyond the middle; costal veinlets not clearly preserved, mostly simple over the apical portion; *Sc* and R_1 fused towards the apex and there bent parallel to the costal margin; *Rs* with 8 major branches, not counting *MA*; *MA* fused to *Rs* for a very short distance and its proximal portion appearing almost transverse, though slightly oblique; *MA* well forked towards the wing margin; *MP* forked after the freeing of *MA* from *Rs* and both branches deeply forked, particularly M_{3+4}; *CuA* with 4 main pectinate branches towards the margin; *CuP* very deeply forked; anal veins with short pectinate branches towards the margin; crossveins not clearly preserved, apparently of limited number between R_1 and *Rs*.

Type.—Holotype forewing C785 and counterpart C784 in the University of Queensland, Department of Geology collection.

There are no additional specimens. The species differs only slightly from the genotype, mainly in the deeper forking of *CuP* and the pectination of *CuA*.

ARCHEOSMYLUS ? COSTALIS, sp. nov.

Plate 3, Fig. 4; Fig. 21

Forewing: Wing rather small, length of preserved portion of holotype 8 mm, indicating a total length of about 11 mm; costal space markedly expanded in the middle, narrowing rather rapidly towards the apex; apex not preserved; costal veinlets numerous, at least some forked over the middle portion but the apical half simple; *Rs* with 6 major branches, not counting *MA* which is fused to *Rs* for some distance, 2 of them deeply forked; basal stem of *MA* not preserved; *MP* forking after the origin of *MA* from *Rs*, the upper branch remaining simple almost to the wing margin, but M_{3+4} forking normally and with the usual end-twigging; *CuA* with 4 or more terminal pectinate branches; *CuP* deeply forked; crossveins not all clearly preserved, but an outer and an inner gradate series present and a few, other, more basad ones.

Type.—Holotype forewing fragment C907 and counterpart C908 in the University of Queensland, Department of Geology collection.

There are several additional specimens but all are very fragmentary and referred only doubtfully to the species (C2198-9; C1761-2; C1941-2; C1166-7; C823-4).

The species, although imperfectly known, is placed in this genus mainly on the fusion between *MA* and *Rs*. The structure of MP_{1+2} is rather distinctive.

Family **OSMYLIDAE**

Subfamily **KEMPYNINAE** Carpenter

In this subfamily *MP* in the forewing is forked at a point slightly beyond the separation of *MA* from *Rs*; in the hindwing *CuP* is long and the proximal part of *MA* is fully developed, with the anastomosed part of *MA* and *Rs* at most only slightly longer than the free basal part.

A new genus described here is placed in this subfamily, although it shows rather more primitive characters. In particular, in the forewing, the proximal part of *MA* is fully formed and only just touches *Rs*, not being fused to it for any length.

Genus LITHOSMYLIDIA, gen. nov.

Genotype *Lithosmylidia lineata*, sp. nov.

Closely allied to *Lithosmylus* Carpenter (1943), but differing, in the forewing, chiefly in retaining the free oblique basal stem of *MA*, with that vein only just touching *Rs* and not fused to it for any length. The crossveins of the basal portion of *Rs* are limited, the pterostigmatic veinlets are often forked and the terminal branches of *CuA* and *CuP* are not as transverse.

At first, one might consider this the hindwing, but it shows the late forking of *MP*. Further, the more expanded hindwing of the species is preserved, though it lacks the critical basal structure. In *Lithosmylus* there is a "crossvein" from *MP* to *Rs* corresponding rather closely to the proximal part of *MA*, and *MA* arises from *Rs* almost immediately after this "crossvein".

LITHOSMYLIDIA LINEATA, sp. nov.

Plate 3, Figs. 7-9; Fig. 22

Forewing: Wing rather large, length of holotype 20 mm, indicating a total length of about 25 mm, apex slightly pointed, base not preserved, anterior and posterior margins indefinite, *Sc* and R_1 fused towards apex and there strongly bent down and round towards apex; *Rs* with numerous branches, about 15, simple except towards margin and there slightly twigged; *MA* arising from the stem of *M* before the origin of *Rs*, running obliquely towards the stem of *Rs* and just touching that vein, continuing normally to the wing margin, there slightly twigged; *MP* forked well after the freeing of *Rs* and *MA* and each branch distinctly forked again towards the margin; *CuA* with a pectinate series of 6 major branches towards margin; *CuP* deeply forked; 1*A* deeply forked and with additional branches; crossveins between R_1 and *Rs* apparently not abundant, an outer gradate series and a more indefinite inner series, with additional more basad crossveins and a few in the cubital and anal areas.

Type.—Holotype forewing C2189 and counterpart C2190 in the University of Queensland, Department of Geology collection.

There are two additional specimens. C1642-3 is considered to be the apical half of a hindwing. It is broader, has a more rounded apex and the pterostigma does not extend as far round towards the apex. C867-8 is a fragmentary forewing. C2088-9 and C786-7 are very fragmentary and referred only very doubtfully to this species.

LITHOSMYLIDIA PARVULA, sp. nov.

Forewing: Wing rather small, length 15 mm; apex rounded, with only a very slight pointing, costal space expanded over basal half, narrowing towards apex, greatest width about the middle; costal veinlets forked over the middle portion and at the apex in the pterostigma; *Rs*, *MA*, and forking of *MP* as in the genotype; *CuA* with possibly only 5 apical branches; *CuP* more dichotomously branched; 1*A* deeply forked, 2*A* with a pectinate series, 3*A* with small pectinate branches.

Type.—Holotype forewing C1029 and counterpart C1030 in the University of Queensland, Department of Geology collection.

There are two additional specimens. C1991-2 is a perfect wing but, like the holotype, it is not very clearly preserved. C2092-3 is almost perfect but again indistinct. The fragmentary C1039-40 is referred only doubtfully to the species.

This species is separated from the genotype mainly on its much smaller size. The differences may possibly be sexual, but as there are series of specimens of each size they have been kept distinct.

Family **OSMYLOPSYCHOPIDAE**, fam. nov.

Resembling Recent Psychopsidae, but without the specialized vena triplica found in that family; with a simpler *CuP* and less specialized crossveins. *Sc* and R_1 fused at their apices. The family differs from the Prohemerobiidae in having *Sc* and R_1 fused at their apices. This family would include also *Mesopolystoechus* Martynov (1937) from the Lias.

Genus OSMYLOPSYCHOPS Tillyard

Osmylopsychops Tillyard, 1923, Proc. Linn. Soc. N.S.W. 48: 496.

Genotype *Osmylopsychops spillerae* Tillyard, 1923, loc. cit.

The genus is characterized by the abundantly branched veins, the fused apices of *Sc* and R_1, and the many branched, more or less pectinate *CuA*. *Sc*, R_1, and *Rs* are separate almost to the base, end-twigging is rather limited, costal veinlets are mainly forked and connected by scattered crossveins, and *CuP* and the anals are well branched.

OSMYLOPSYCHOPS SPILLERAE Tillyard

Plate 3, Fig. 6

Osmylopsychops spillerae Tillyard, 1923, Proc. Linn. Soc. N.S.W. 48: 496.

Tillyard has given a description and a restoration of the forewing of this species, which was discovered at the Denmark Hill horizon of the Ipswich Series. The specimens from the Mt. Crosby horizon are considered conspecific. In one of these latter specimens even the cell on M_{3+4} present in the holotype, is preserved. Tillyard's restoration is not quite accurate, as can be seen from his two figures. The costal space should be a little narrower at the fusion of *Sc* and R_1 and there should be a few scattered crossveins connecting the costal veinlets. The wing may not be as pointed at the apex as restored and the presence of a recurrent humeral vein is doubtful.

Types.—Holotype and paratype forewing fragments in the Queensland Geological Survey.

Type locality.—Denmark Hill, Ipswich Series.

Specimens from Mt. Crosby.—C1921 and counterpart of same number lacks both base and apex but is otherwise well preserved; C2187-8 is similar but preserves more of the anal veins; C1523-4 is more fragmentary.

There is some variation in the forking of *CuA* and *M*. The large size of the species (more than 25 mm), and the very numerous veins are distinctive.

Genus ARCHEPSYCHOPS Tillyard

Archepsychops Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 205.

Genotype *Archepsychops triassica* Tillyard, 1919, op. cit. 206.

Forewing: Costal space markedly expanded towards the base but tapering rapidly towards the pterostigma. *Sc*, R_1, and *Rs* probably forming a vena triplica.

This genus was originally placed in the Prohemerobiidae, but was removed to the Psychopsidae by Tillyard in 1922. Although imperfectly known, it seems best considered in the Osmylopsychopidae. It is even possible that *Osmylopsychops* is a synonym of it.

ARCHEPSYCHOPS TRIASSICA Tillyard

Plate 3, Fig. 5

Archepsychops triassica Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 206.

There is a fragmentary specimen, C679, probably of this species, from the Mt. Crosby beds. It preserves little more detail than the holotype, except for the much-branched anals. Although it is from a different horizon of the Ipswich Series, it is tentatively placed in this species.

Type.—Holotype fragment in the Queensland Geological Survey.

Type Locality.—Denmark Hill, Ipswich Series.

Order **ORTHOPTERA (SALTATORIA)**

The Orthoptera (Saltatoria) are of particular interest. Both the Ensifera and the Acridodea are represented, though there is only one species belonging to the latter. This is *Triassolocusta leptoptera* Tillyard (1922*a*), the oldest representative of the extinct family Locustopsidae, which contains the most primitive of the true Acridodea. The Ensifera are more abundant, with representatives of the two primitive families, Prophalangopsidae and Gryllacrididae. The Prophalangopsidae are mainly of Jurassic age, but there are two living genera (Zeuner 1939). One South American genus is recorded from the Triassic and two new ones are described here. One represents a most primitive type, which is probably ancestral to both this family and the Gryllacrididae. True Gryllacrididae are represented by two quite distinct types belonging to the Gryllacridinae. Although these represent the oldest record of the family they are more specialized than the primitive Palaeorehniinae, which is recorded first from the Jurassic. A new family is erected for a species somewhat allied to the Geinitziidae. In both families *Rs* is directed anteriorly, but in this species *MA* and *Rs* are partially fused and *Cu* is strongly developed and much branched. Its affinities are somewhat doubtful. From the above remarks it is evident that the Orthoptera (Saltatoria) from these beds are phylogenetically very interesting.

Suborder **ACRIDODEA**

Family **LOCUSTOPSIDAE** Handlirsch

Genus TRIASSOLOCUSTA Tillyard

Triassolocusta Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 451.

Genotype *Triassolocusta leptoptera* Tillyard, loc. cit.

TRIASSOLOCUSTA LEPTOPTERA ? Tillyard

Fig. 23

Triassolocusta leptoptera Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 451.

There is a fragment, No. C6, doubtfully referred to this species. The preserved portion differs somewhat from the holotype in the structure of *Sc*, but the origin and 1st forking of *Rs* and the forking of *M* are similar.

At the wing margin between the branches of *M* there are short intercalated veins. C43, which is even more fragmentary, may possibly belong here.

Suborder **ENSIFERA**

Family **PROPHALANGOPSIDAE** Handlirsch

Subfamily **PROHAGLINAE** Riek

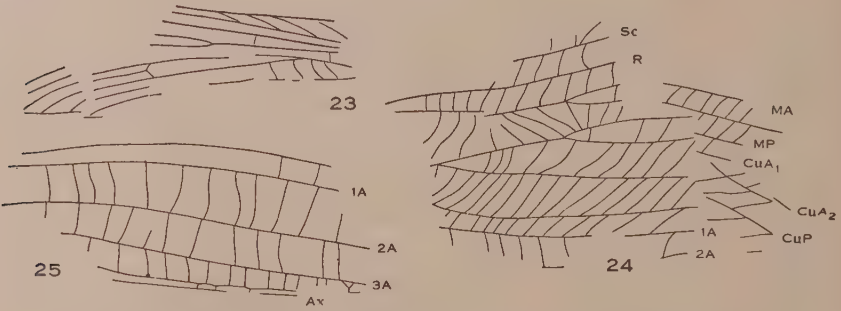
This subfamily was erected for *Prohagla* Riek (1954) from the Triassic beds at Brookvale, New South Wales. A species referred to the same genus is recorded in this paper from the Mt. Crosby beds.

Genus PROHAGLA Riek

Prohagla Riek, 1954, Rec. Austr. Mus. 23: 164.

Genotype *Prohagla superba* Riek, 1954, loc. cit.

The genotypic species is known from perfect fore- and hindwings and both sexes have been recognized. The present species is rather imperfectly known and the fragmentary holotype is considered to belong to a female specimen.



All figures *c* × 4.

Fig. 23.—C6, *Triassolocusta leptoptera* ?Tillyard, wing fragment.

Fig. 24.—C72, holotype of *Prohagla imperfecta*, sp. nov.

Fig. 25.—C1971, *P. imperfecta*, anal area of wing.

PROHAGLA IMPERFECTA, sp. nov.

Plate 4, Fig. 5; Figs. 24, 25

All the specimens are rather fragmentary. The description is based mainly on the holotype, C72, but the anal veins are described from C1971 and C2120. These seem to belong to a somewhat larger specimen than the holotype.

Forewing: ? Female. None of the wing margin preserved. Preserved portion of *Sc, R,* and *MA* similar to genotype; lower branch of *M* (*MP*) running to CuA_1 not sharply differentiated from the crossveins of the area, fused to CuA_1 at least for some distance, distal portion not preserved; *Cu* with *CuP*, CuA_2, and 2 distal branches, but more distal branching to the wing margin not preserved; stem of CuA_1 almost straight, not arched towards M, CuA_2 rather straight, more or less parallel to lower branch of CuA_1, CuP well separated from CuA_2, not strongly arched away from it over its middle portion (giving further indication that the specimen is a female); first anal close to CuP, almost parallel to it, 2nd and 3rd anals widely spaced, only very gentle curve, curvature not markedly sigmoidal; 4th anal (or axillary) not widely spaced from 3rd anal, very close to the wing margin.

Type.—Holotype, fragment of a forewing, C72 and counterpart C73. Paratypes, C1971; C2120; C1450-1; and C1190-1-2. All specimens in the University of Queensland, Department of Geology collection.

It is possible that this is merely another female of *superba* with the cubital area of the wing not markedly expanded, but as the two species are from widely separated localities and distinct horizons they are best considered separately.

PROHAGLA, sp. indet.

There are two fragmentary remains of a smaller species, probably referable to this genus. C820-1-2, preserves the apical portion of Sc and most of R_1 and Rs. C267 shows the anals and portion of Cu.

Subfamily **HAGLINAE** Zeuner

A primitive subfamily with only slight modification of the wing for stridulation. Except for the primitive *Prohagla* Riek, this subfamily contains the most primitive forms, derived very probably from a sthenaropodid-like stock in the Palaeozoic.

Genus NEOHAGLA, gen. nov.

Genotype *Neohagla sinuata*, sp. nov.

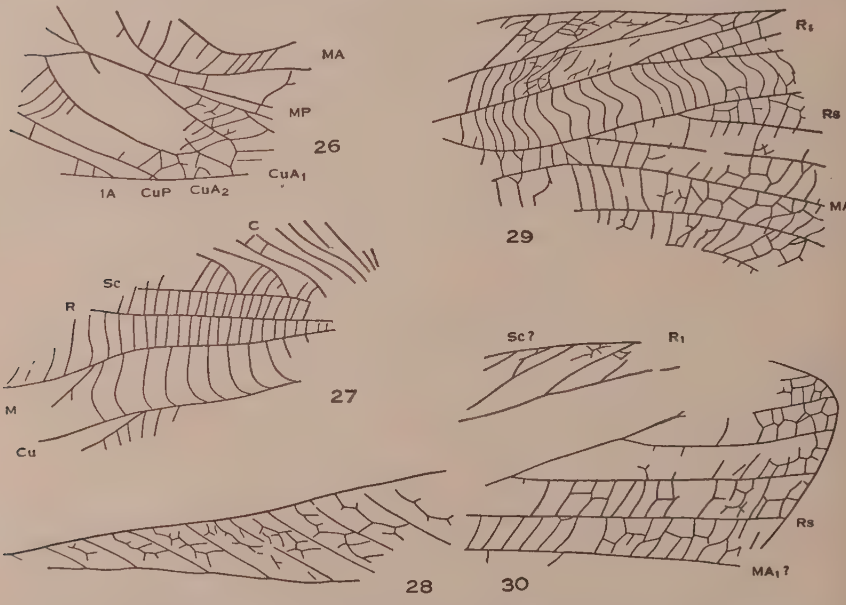
Only the almost complete forewing of the male is known. The genus is closely allied to *Hagla* Giebel from the Lias of England, but retains a more primitive character in the reduced branching of R_1. Also, in *Neohagla*, MP and Cu fuse only after the origin of CuA_2 and the crossveins between R_1 and Rs are more sinuous. Anal area not preserved.

NEOHAGLA SINUATA, sp. nov.

Plate 4, Figs. 2-4; Figs. 26-30

The almost complete structure of the forewing of the male, except for the anals, is known from five fragmentary specimens. The description of the apical half is based on C1892 and to some extent on C1893. The more basad portion of the costal margin is added from C2204; the cubital field and branching of M from C2216; the basal portion of the wing from C2220; and portion of the anal veins from C1455.

Forewing: *Male.*—Wing rather large, apex slightly pointed, costal space markedly expanded over the basal half, narrowing rather rapidly towards the apex. *C* with a number of short, radiating branches, not extending far along the costal border; *Sc* with numerous, oblique veinlets to the wing margin, with the crossveins forming an irregular archedictyon; *Sc* and *R* connected basally by strong, straight, transverse crossveins as also are *R* and *M*; *Rs* arising at about the middle of the wing, R_1 almost parallel to *Sc*, forking near the apex of *Sc*, with 2, and possibly 3, oblique anterior branches to the wing margin; *Rs* diverging rapidly from R_1, the 2 well separated but converging towards the apex, *Rs* with a pectinate series of 5, almost parallel, branches; *M* arising from the base, forking slightly after *Cu*, with the upper branch, *MA*, forking again very soon, with both branches strongly sinuate, particularly MA_1, which approaches rather closely to the stem of *Rs* and then continues almost parallel to R_5, *MP* fused to *Cu* for some distance after the origin of CuA_2 but separating well before the wing margin; CuA_1 with at least 3 branches, CuA_2 widely separated from CuA_1, sigmoidally curved, *CuP* widely separated from CuA_2 at the origin of that vein but approaching it towards the apex; 1*A* preserved only at the wing margin, close to *CuP*. Crossveins numerous, at the base and centre of the wing simple, but towards the wing margin



Neohagla sinuata, sp. nov. All figures *c.* × 4.
Fig. 26.—C2216, holotype, preserving parts of the cubital and median fields.
Fig. 27.—C2220, basal portion of the wing.
Fig. 28.—C2204, costal region.
Fig. 29.—C1892, most of apical half.
Fig. 30.—C1893, apical portion.

more irregular; the long simple crossveins between R_1 and Rs basally strongly curved, often irregularly so; the crossveins between M and Cu basally long, widely spaced, and gently curved.

Types.—Holotype, fragment of male forewing, C2216 and counterpart C2217 preserving only the diagnostic portion of the cubital and median fields; paratypes C1892 and counterpart C1891, most of apical half; C1893-4 shows the shape at the apex; C2204 and counterpart C2205 preserves most of the costal margin and costal space; C2220 and counterpart C2219 preserves the basal structures; and C1455 and counterpart C1454 preserves portions of the anal veins. C1735 and counterpart C1736, and C1804 and counterpart C1805, are very fragmentary. All specimens in the University of Queensland, Department of Geology collection.

The species has been reconstructed from several very fragmentary specimens, but little doubt is felt that they all belong to the one species, though possibly not to the one sex. The holotype clearly places the species in the subfamily Haglinae which is considerably more highly evolved than the Prohaglinae, the other subfamily represented in these beds.

Family **GRYLLACRIDIDAE** Stål

Subfamily **GRYLLACRIDINAE**

This is one of the subfamilies which retains such primitive features as a generalized venation. The new genus, placed in this subfamily, belongs in the group of genera with the most primitive type of venation. Rs and M do not touch, both M and Cu are 2-branched and do not touch. It differs from all other members of the subfamily in the shorter C and more primitive Sc. In these characters it approaches *Jurassobatea* Zeuner (1939) of the most primitive subfamily Palaeorehniinae which, however, is known no earlier than the Jurassic. The new genus *Mesogryllacris* is the oldest representative of the family.

Genus MESOGRYLLACRIS, gen. nov.

Genotype *Mesogryllacris giganteus*, sp. nov.

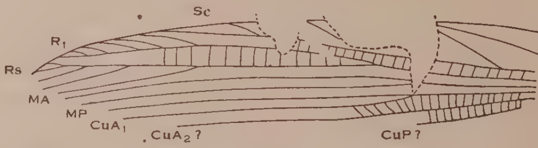
Forewing: Costal margin expanded at base, C strong, but short, only a quarter of the wing length; costal space with a number of costal veinlets, R_1 giving off an anterior series of short branches to the wing margin beyond Sc, Rs arising towards the basal third of the wing, with a series of pectinate branches over its apical half; M 2-branched, forking in the basal half of the wing, not touching Rs; Cu 2-branched, not partially fused with the posterior branch of M, forking at a level with the forking of M, succeeding veins long and simple.

MESOGRYLLACRIS GIGANTEUS, sp. nov.

Plate 4, Fig. 1; Fig. 31

Forewing: Wing large, length 60 mm; anterior margin convex, apex rounded, expanded at base; C strong, short; Sc long, extending to the apical quarter of wing, with an anterior series of oblique veinlets to the wing margin; R_1 almost parallel to *Sc*, ending just before the apex of the wing, with a series of 5, short, anterior branches to the wing margin beyond *Sc*; *Rs* forming a series of 5 pectinate branches over its apical half; *M* forking before the origin of *Rs*; *Cu* forking at almost the same level as *M*, the branches of *M* and *Cu* very long, continuing parallel to the wing margin, *CuP*? (or 1*A*) simple, rather widely separated from *Cu* near its base, succeeding vein with only the basal portion preserved.

Types.—Holotype, forewing, in three fragments, C1920, C1544, and C1930, glued together to form an almost complete wing except for the anals, and the counterpart, in two pieces, C1929 and C1919. There is a paratype fragment C2120. C1543 is referred only doubtfully to this species. All specimens in the University of Queensland, Department of Geology collection.



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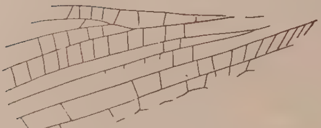
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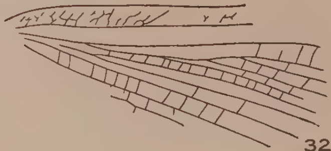
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Fig. 31.—C1920, holotype of *Mesogryllacris giganteus*, sp. nov. *c.* × 1.5.
Fig. 32.—C2214, holotype of *Xenogryllacris reductus*, sp. nov. *c.* × 5.
Fig. 33.—C31, paratype of *X. reductus*, sp. nov.

The wing is of rather large size, at first glance recalling that of the female *Clathrotitan* McKeown (1937), but the structure is rather different.

Genus XENOGRYLLACRIS, gen. nov.

Genotype *Xenogryllacris reductus*, sp. nov.

This genus has the modified type of venation, with *M* fused basally with *Rs*, for some distance as in the Recent *Dictyogryllacris* but the costal space is not expanded at the base as in Recent genera. Although the specimen on which the genus is based is very fragmentary, it preserves the diagnostic area of the wing. Together with *Mesogryllacris* described above, it is the oldest known gryllacridid. It is considered important to record that two such diverse types of venation were present even at this early period.

XENOGRYLLACRIS REDUCTUS, sp. nov.

Plate 4, Fig. 7; Figs. 32, 33

Forewing: Wing very fragmentary, only the basal half from the costal margin to *CuP* preserved. Costal space narrow, very slightly expanded near base. Between *Sc* (or *C*) and the costal margin a series of irregular crossveins forming an anastomosing network; R_1 poorly preserved, well separated from *Sc* (or *C*); *Rs* arising fairly close to the base, stem of moderate length, apical portion of *Rs* not preserved; *MA* unbranched, arising from the stem of *Rs* rather close to its 1st forking; *MP* and *CuA* separating very close to the base, the 2 branches running parallel, close together, *CuP* ? straight, more spaced from *CuA* than *CuA* and *MP* are separated, succeeding vein strong, parallel to, but well separated from, *CuP* ?.

Types.—Holotype fragment C2214 and counterpart C2213. Paratypes C31 and counterpart C10; C1820-1 and C1965-6. All specimens in the University of Queensland, Department of Geology collection.

The fragment is imperfect, but the preserved characters are distinctive, at least of that group of genera with venation similar to *Dictyogryllacris* (see Zeuner 1939).

Family **XENOPTERIDAE**, fam. nov.

Only forewing known. Allied to the Geinitziidae (Zeuner 1939) where *Rs* is directed anteriorly but *MA* and *Rs* are partially fused; *Cu* with many branches, particularly CuA_3.

There is some resemblance to *Triassomantis* Tillyard (1922) from the Trias of Denmark Hill, but that species is rather imperfectly known.

Genus XENOPTERUM, gen. nov.

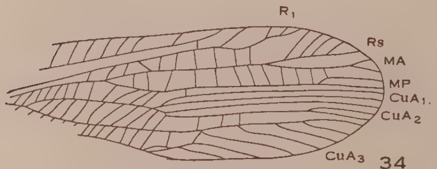
Genotype *Xenopterum crosbyi*, sp. nov.

Forewing: R_1 sigmoidally curved almost at the apex; *MA* separating from *Rs* before *Rs* gives rise to the anteriorly directed pectinate branches; *MP* normally simple or only branched near the wing margin; CuA_1 and CuA_2 forming a series of closely placed, parallel branches, rarely branched near the wing margin, CuA_3 giving off a posterior series of pectinate branches, *CuP* also pectinately branched; anals not preserved.

XENOPTERUM CROSBYI, sp. nov.

Plate 4, Fig. 6; Figs. 34-37, 38

Forewing: Wing of moderate size, length of preserved portions up to 13 mm, indicating a total length of almost 20 mm; *Sc* ending well before the apex of the wing; costal veinlets numerous, simple; R_1 almost parallel to *Sc*, with a limited number of branches to the costal margin; *Rs* apparently forking about the middle of the wing, almost immediately fusing with *MA*, giving off, near its apex, a series of from 4-6, short, parallel, anterior branches to the wing margin; *M* forking just before the origin of *Rs,* with *MA* fusing with *Rs,* but separating again just before the forking of *Rs,* and forked close to the margin, *MP* continuing almost to the wing margin before forking; *CuA* forking early into 2 widely separated branches connected by strong crossveins over their basal halves, CuA_{1+2} branching, twice, almost at the one point, to give rise to 4 (or rarely 5), close, parallel branches somewhat before its middle, CuA_3 giving off a series of 4 or 5 curved branches after the forking of CuA_1 and CuA_2; origin of *CuP* not preserved, with 2 or 3 anteriorly arched branches at the wing margin; anals not preserved.



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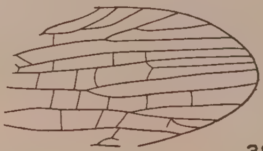

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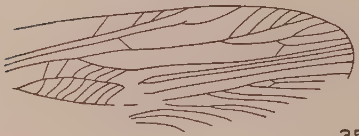

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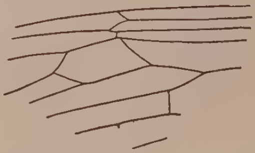

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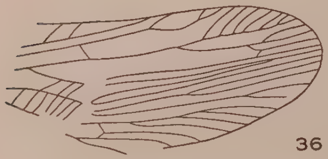

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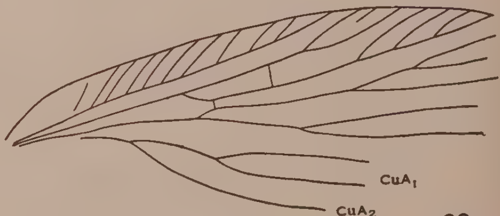

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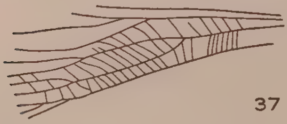

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All figures *c.* × 4.
Fig. 34.—C2066, holotype of *Xenopterum crosbyi,* sp. nov.
Fig. 35.—C768, *X. crosbyi,* sp. nov.
Fig. 36.—C1962, *X. crosbyi,* sp. nov.
Fig. 37.—C2208, *X. crosbyi*?
Fig. 38.—C1758, incertae sedis.
Fig. 39.—C2142, fragment of a protorthopteron.
Fig. 40.—C1959, ?*Stenoperlidium* sp.

Type.—Holotype C2066 and counterpart C2067 in the University of Queensland, Department of Geology collection.

There are numerous additional (paratype) specimens. C768-9 and C1961-2 are almost as well preserved as the holotype. C2206-7; C1832;

C1969-70; C487-8; C1837; C1972; C2099; C2105; C1215-6; C571; C1620; C1739-40; C2215; C2212; and C2210-11 are more fragmentary. C2208-9 shows a slightly different structure and is referred only doubtfully to this species.

This species is rather problematical. The strongly developed cross-veins in the middle of the wing are similar to those of Perlaria and some Orthoptera. The close, parallel branches of *MP* are characteristic, but do not seem to ally the species to any known group. The wing has the facies of the Protoperlaria, but there are many obvious differences.

Order **PROTORTHOPTERA**

Fig. 39

There is a fragmentary specimen of a species belonging to this order. In many features it recalls *Liomopterum* Sellards from the Lower Permian of Kansas (Carpenter 1950), but the branching of R_1 and *Rs* are quite distinctive (see Fig. 39). As the specimen, C2142, is not well preserved, no specific description is given. This is the second record of the order persisting into the Triassic in Australia, *Austroidelia perplexa* Riek (1954) having been described from the Triassic at Brookvale, New South Wales.

Order **PERLARIA**

Family **EUSTHENIIDAE**

Genus STENOPERLIDIUM Tillyard

Stenoperlidium Tillyard, 1935, Proc. Linn. Soc. N.S.W. **60**: 386.

Genotype *Stenoperlidium permianum* Tillyard, 1935, op. cit. 387.

The genotype is from the Upper Permian of Belmont, New South Wales. This genus, or a closely allied one, is present in the Mt. Crosby fauna, but it is too fragmentary for specific diagnosis.

? STENOPERLIDIUM sp.

Fig. 40

Fragment: C1959 and counterpart C1960 preserves the middle portion of a wing, from just basad of the forking of *M* to just beyond the 1st forking of *Rs*.

Order **ODONATA**

Only two very fragmentary specimens of Odonata, C1536-7 and C1538-9, have so far been discovered in these beds. They are mentioned merely to indicate the presence of an odonate element in the preserved insect fauna.

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PLATE 1

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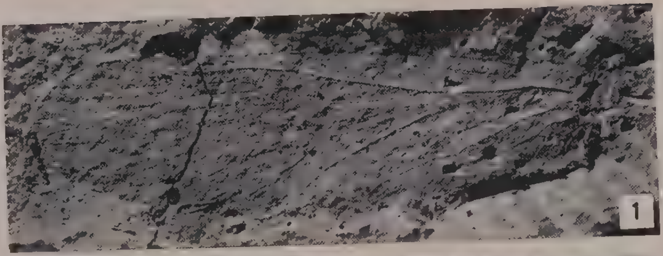
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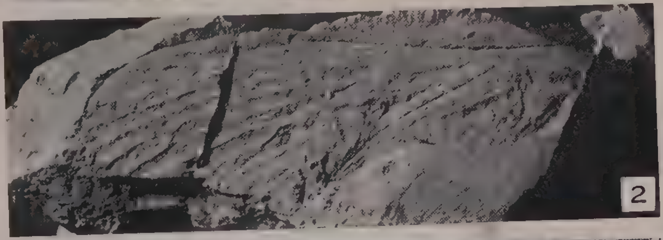
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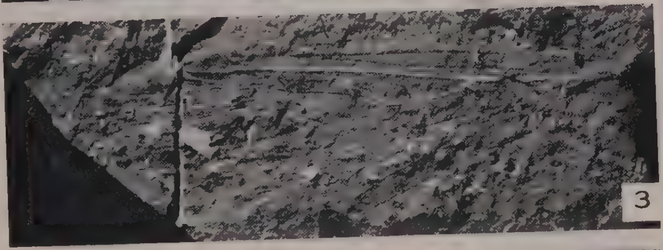
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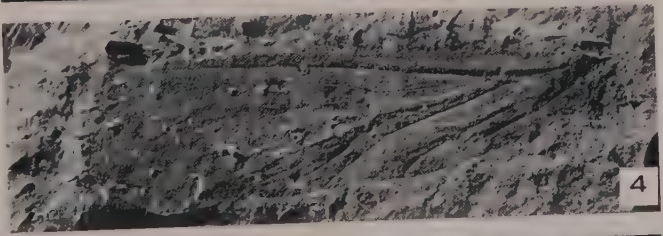
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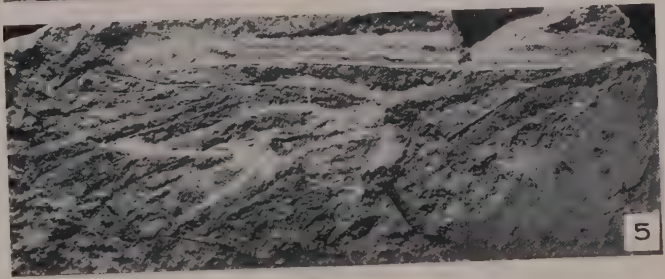
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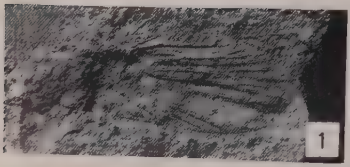
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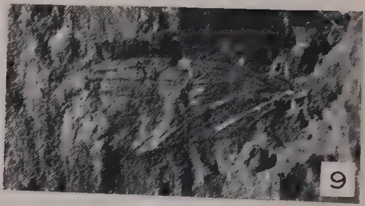
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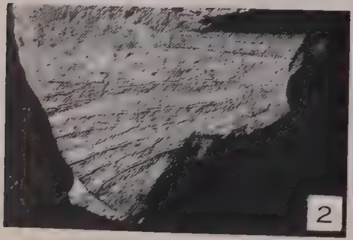
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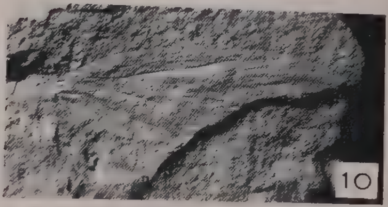
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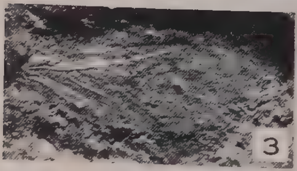
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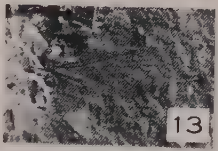
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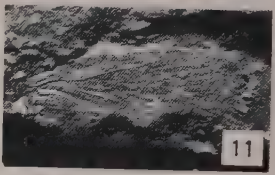
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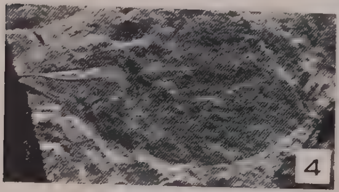
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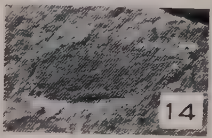
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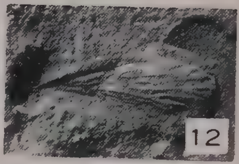
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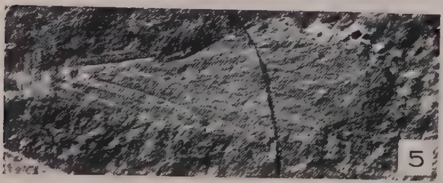
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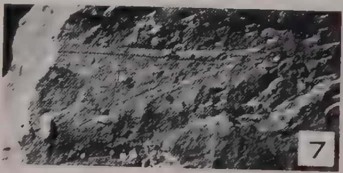
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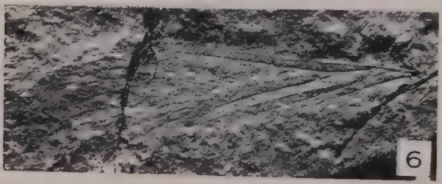
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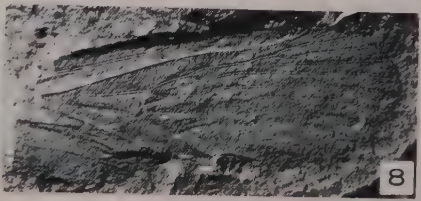
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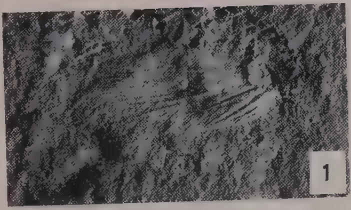

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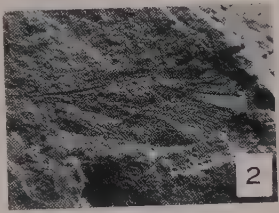

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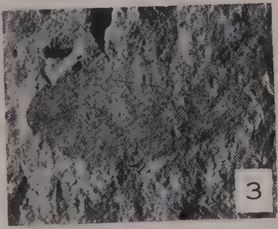

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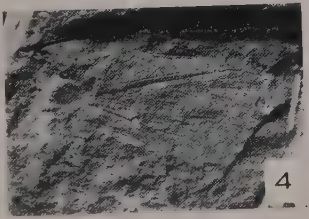

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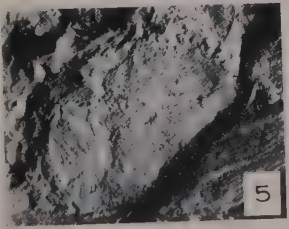

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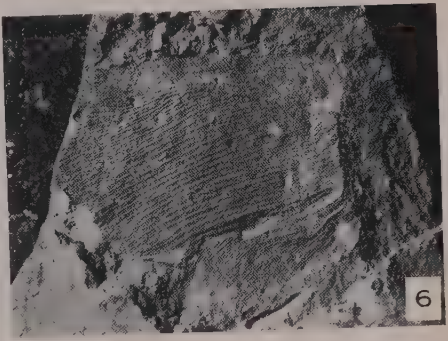

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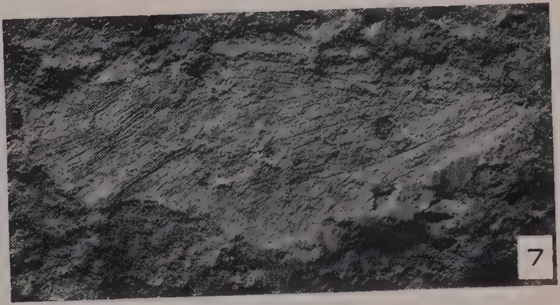

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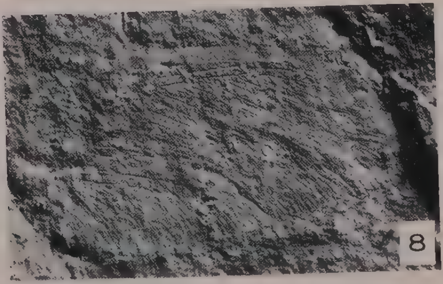

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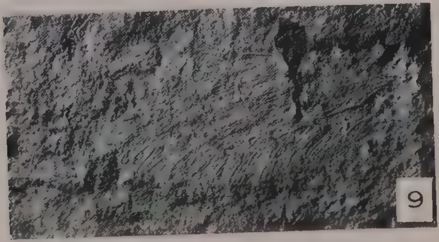

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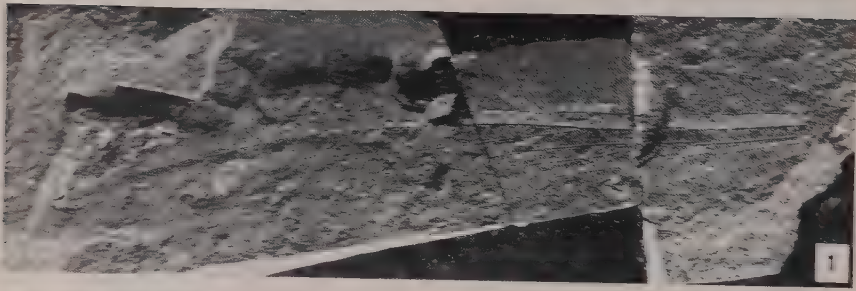

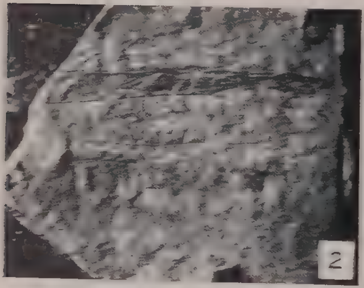

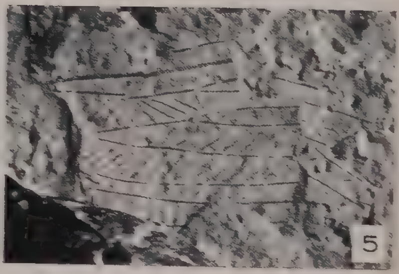

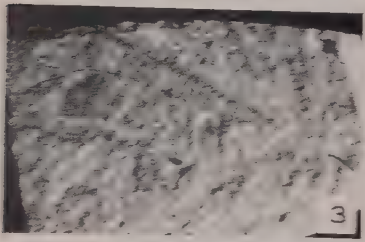

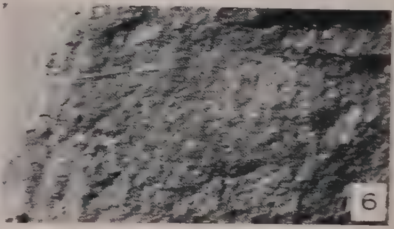

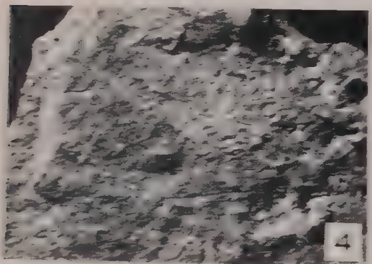

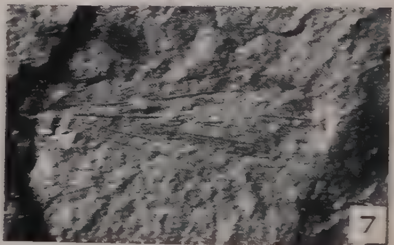

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EXPLANATION OF PLATES 1-4

PLATE 1

All figures *c.* × 4.

Fig. 1.—*Neoparachorista perkinsi*, gen. et sp. nov., holotype, C1897.
Fig. 2.—*Neoparachorista perkinsi*, paratype, C735.
Fig. 3.—*Neoparachorista perkinsi*, hindwing, C2145.
Fig. 4.—*Neoparachorista splendida*, sp. nov., holotype, C1889.
Fig. 5.—*Neoparachorista semiovena*, sp. nov., holotype, C1760.

PLATE 2

All figures *c.* × 4.

Fig. 1.—*Neopermopanorpa mesembria*, gen. et sp. nov., holotype, C643.
Fig. 2.—*Xenopanorpa didymovena*, gen. et sp. nov., holotype, C1043.
Fig. 3.—*Mesochorista proavita* Tillyard, C2248.
Fig. 4.—*Mesochorista proavita* Tillyard, C808.
Fig. 5.—*Archebittacus exilis*, gen. et sp. nov., counterpart of holotype, C2140.
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Fig. 8.—*Neoparachorista perkinsi*, gen. et sp. nov., abnormal specimen, C1907.
Fig. 9.—*Xenochoristella hillae*, gen. et sp. nov., holotype, C2115.
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Fig. 11.—*Cladochoristella bryani*, variant on media, C.710.
Fig. 12.—*Cladochoristella bryani*, variant on the apex of *Sc*, C882.
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Fig. 14.—*Mesotanyderus jonesi*, gen. et sp. nov., holotype, C1054.

PLATE 3

All figures *c.* × 4.

Fig. 1.—*Proberotha superba*, gen. et sp. nov., holotype, C1404.
Fig. 2.—*Proberothella elongata*, gen. et sp. nov., holotype, C2196.
Fig. 3.—*Archeosmylus stigmatus*, sp. nov., holotype, C785.
Fig. 4.—*Archeosmylus ? costalis*, sp. nov., holotype, C907.
Fig. 5.—*Archepsychops triassica* Tillyard, C679.
Fig. 6.—*Osmylopsychops spillerae* Tillyard, C1921.
Fig. 7.—*Lithosmylidia lineata*, gen. et sp. nov., holotype, C2189.
Fig. 8.—*Lithosmylidia lineata*, apex of hindwing, C1642.
Fig. 9.—*Lithosmylidia lineata*, forewing, C867.

PLATE 4

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Fig. 1.—*Mesogryllacris giganteus*, gen. et sp. nov., holotype, C1920-1544-1930.
Fig. 2.—*Neohagla sinuata*, gen. et sp. nov., apical portion, C1892.
Fig. 3.—*Neohagla sinuata*, gen. et sp. nov., basal portion, C2220.
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